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DIPLOBLASTIC ANIMALS

By Dr C. F. A. Pantin, F.R.S.

(With Plates 1–4 and 2 Text-figs)

From ancient times men have perceived that living creatures are disposed in grades of organization, which differ both in degree and in kind. Until the end of the 18th century some even attempted still to arrange these grades in a single series, a *scala naturae*; with Man at the top, ranging down through fishes, worms, zoophytes and plants to the productions of the mineral kingdom. That great comparative anatomist Cuvier showed that there was no such single series: there were several distinct types of animal organization. Nevertheless the idea of grades of increasing complexity remained, and still remains. The notion is not baseless: when we say that man is a higher grade of organism than an earthworm, and that an earthworm is higher than a sea-anemone, and that in turn a sea-anemone is higher than a protozoan we are giving expression to a subjective judgement which, though difficult to define, certainly contains an element of truth.

When we look at the animal kingdom there are two primary grades of organization, that of the unicellular—or non-cellular—Protozoa, and that of the Metazoa the bodies of which are composed of cells. I shall not discuss to-day that interesting and apparently independent development of cellular organization that we see in the sponges; nor those somewhat rare and enigmatical parasites the Mesozoa. Of the remaining cellular animals, the Eumetazoa (cf. Hyman, 1940), one phylum stands out as of simpler organization than the others, that is a group which includes the Hydroids, the Medusae and the Anthozoa or sea-anemones. Following Hyman's classification, we will refer to this group as the Coelenterata (or Cnidaria) which together with the Ctenophora comprize the Radiata.

The simplicity of a Coelenterate is the simplicity of the tissues of which it is composed. In contrast, a Nematode worm is simple, but this is because of the simplicity in the number and relation of its highly differentiated organs. In the Coelenterata, Thomas Henry Huxley showed in 1849, that the body wall of a Medusa, which encloses the cavity of the gut, consists essentially of two 'foundation membranes'. That was also found to be true of Hydroids and of the Anthozoa. Soon after, in 1853, Allman, near the beginning of his great researches on the hydroids, wrote:—

> All hydroid zoophytes can be proved to consist essentially of two distinct membranes; to the external of these membranes I shall give the name of *ectoderm*, and to the internal that of *endoderm*.

That is the original definition of these terms.

Between these two membranes of the body-wall lies a gelatinous or fibrous substance, the *mesogloea*. This as we now know consists of collagen, and its staining reactions also suggest the presence of muco-polysaccharides, as in the connective tissue of the higher animals. I shall speak later of the cellular elements which the mesogloea may sometimes possess. Often it contains none, and has even been referred to as a ' structureless lamella ' (Sedgwick, 1898) Structureless it cannot be, and electron-microscopical studies always show that it is fibrous, as its mechanical properties indicate that it must be (Chapman, 1953).

The mesogloea differs considerably in appearance in different Coelenterates. The fibrous structure of a sea-anemone is coarse. That of Hydra is ultramicroscopic (Hess, Cohen & Robson, 1957). In both cases it is highly extensible. Medusae possess a gelatinous ' elastic ' mesogloea which is easily distorted but relatively inextensible. As Chapman (1953) has shown, it contains few fibres, and these are more or less arranged as a system of radial tensors acting against the pressure of the mesogloeal fluid which bathes the collagen fibres. In life, Medusae maintain turgor in the mesogloea by this fluid. Damage to the ectoderm is soon followed by collapse of the jelly, so that the attached muscle can no longer function properly. It is noteworthy that masses of isolated ectoderm cells of the hydroid *Cordylophora lacustris* Allman form an internal cavity into which they secrete fluid (Beadle & Booth, 1938).

Differences in appearance and in mechanical properties have led to terminological differences for different sorts of mesogloea : collenchyme, fibrous connective tissue, and so on. There is no harm in this so long as it is remembered that the very different kinds of the mesogloea are easily derivable the one from the other. Like those of Medusae, the fibres of the highly fibrous Anthozoan mesogloea are also bathed in fluid—indeed the extensibility of the collagen lattices of which it is composed depends on this—and we could pass quite easily from this system to that of Medusae by simply distending the mesogloea by increasing its fluid component till the collagen fibres of the lattice are stretched till they span between the two dermal layers.

Thus primarily the body of a Coelenterate consists of a collagen connective tissue, the mesogloea, bounded by two superficial dermal layers, the ectoderm and the endoderm. This two-membraned structure of a Hydroid stands in strong contrast to that of all the higher animals. In these we again find an ectoderm and endoderm, but in place of the mesogloea are masses of tissue of various origin, which compose the mesoderm. If we remove the ectoderm and endoderm from a Coelenterate we are left with little more than a mass of collagen. If we do this to the body of a man or an annelid worm we are left with the bulk of the characteristic organs. For these two grades of organization, the two-layered and the three-layered, Ray Lankester (1873) introduced the terms diploblastic and triploblastic.

There is one further historical point : with characteristic insight Thomas Huxley in his 1849 paper remarked upon the similarity of the relation of the two dermal layers of a Coelenterate to what he called the ' serous and mucous layers of the germ ', that is, of the early stages of the vertebrate embryo.

I have gone into this historically because I want to emphasize the fact that these were pre-Darwinian inferences directly made from comparative anatomy. They were not mere extensions of later evolutionary theory. But after 1859 all these ideas were appropriated by phylogenetic speculation, particularly under the influence of Ernst Haeckel (1874). Then ancestral survivals were to be sought in the simpler grades of living creatures, creatures in which evolution had progressed in leisurely fashion, or not at all, and the corresponding embryonic stages of the higher animals became the equivalent of ancestral forms.

I will only traverse Haeckel's *Gastraea* theory of the evolution of cellular

animals in outline. According to this, undifferentiated primitive protoplasm developed a nucleus and became a cell. This then became divided into colonial aggregations of cells, comparable to Volvocina amongst the algae : and from these in due course there evolved the two-layered Gastraea with a terminal mouth, comparable to the Gastrula of so many embryonic histories. The fresh water Hydra was a living example of this grade.

Beyond the Gastraea, evolution proceeded by the acquisition of the mesoderm between the two primitive layers. This took place in two stages. First there was a wholesale cellular invasion of the mesogloeal space between ectoderm and endoderm. The Turbellarian flat worms were representatives of this stage with their highly developed parenchyma of connective tissue, muscle, nerve and other tissues. Later a new and important mesodermal element was added, the coelomic epithelium. It was derived from the endoderm ; thus were evolved the coelomate higher animals.

Speculative genealogy of this sort was highly vulnerable. It seems clear that cellular animals must have had unicellular ancestors, and that the more complicated cellular animals arose from simpler ones, but several alternative theories arose about the way this happened. Saville Kent (1881) and Adam Sedgwick (1888) suggested that the ancestral metazoan was not a colonial protozoan, but a multinucleated Infusorian-like animal whose differentiated parts were cut off with their nuclei as cells (see also Dobell, 1911). As Sedgwick says, this is indeed the old view of the origin of the Metozoa. In the light of our modern knowledge of infusorian structure, with its peculiarly un-Metazoan organization of skeletal pellicle, basal bodies and ciliary complication, it is not easy to see how this could be easily transformed into the metazoan machinery of internal collagen basement membranes, with their attached muscle fibres below the surface of the animal and into the conducting cell surfaces and synapses which convey and control the nervous impulse and so on. Nevertheless, until we know more about Protistan ultrastructure and see exactly what such an evolutionary change would involve it remains valid as a hypothesis ; though not more so than the alternative, that colonies of cells became differentiated into multicellular organisms. It is difficult to deny that this seems quite evidently what has happened in sponges and in the higher plants. The difficulties raised by Dobell (1911) are difficulties of definition rather than difficulties of fact and will not be discussed here.

Electron microscopy may settle this question. For we now know that far from being the 'primordial slime' of a century ago protoplasm is in fact as full of elaborate adapted machinery as the assembly shops of a factory—nucleus, mitochondria, microsomes, endoplasmic reticulum, and ciliary and other contractile apparatus. When we know more about the rather strange rules of homology at this level of organization, and when we know more about the 'pre-adaptive' potentialities of molecules, like acetyl choline and adrenaline, which occur in protozoa and which come to be utilized in special ways in the cellular machinery of the Metazoa (Pantin, 1951) we may very well find clear evidence about how the cellular animals arose.

Division of opinion in the last century was not confined to the origin of cellularity. Both Ray Lankester (1873, 1877) and Metschnikoff (1879) agreed that the original diploblastic ancestor was not derived by the invagination of a *Volvox*-like blastula but possessed a solid parenchymatous endoderm beneath the ectoderm, like the planula larva of the coelenterates themselves. For in fact the Coelenterate only rarely develop through an invaginate gastrula. They reach their diploblastic condition in an astonishing variety of ways (cf. Hyman, 1940). That is perhaps understandable when we remember that all that has to be done embryonically is to produce somehow or other a two-layered sac. To speak anthropomorphically, natural selection will not mind very much how

that is done. But if, as in many of the higher animals, a gastrula is only the first stage in an elaborate developmental sequence, its formation must surely be stereotyped ; for casual initial variation could have disastrous morphogenetic consequences. The ' ancestral gastrula ' could only gradually come into stereotyped existence. Like the bogus pre-Norman ancestors of some ancient families, the actual forefathers may have enjoyed more variety and less respectability.

Whatever the origin of the two-layered condition, some held that a ' planuloid ' ancestor like that of Lankester and Metschnikoff gave rise directly to the simplest of the Turbellarian worms, the Acoela, (Steinmann & Bresslau, 1913) (Pl. 2A). In these there is no hollow gut, and the ectoderm encloses a solid mass of cells which includes endoderm, capable of ingesting food phagocytically. These Acoela were originally held to be degenerate, but the detection by v. Graff (1882) of certain features in them, such as the possession of some musculo-epithelial cells, caused them to be reconsidered as the most primitive flatworms.

The notion that the Acoela are a primitive stock of animals has recently been revived by Hadzi (1944, 1953). He has in addition made the interesting suggestion that the Cnidaria, or Coelenterata, are not derived directly from a planula-like ancestor but by degeneration from the Turbellaria Acoela. Hydra, and the rest, which were of the very type of the ancestral diploblastic Gastraea of Haeckel are thus degenerate. According to Hadzi the bilaterally symmetrical Turbellaria, which led a free life and possessed free locomotion, gave rise to a sessile radially symmetrical polyp like a sea-anemone—which lost every organ system connected with free locomotion. The protonephridial system disappeared. The nervous system degenerated to mere plexuses. Complex sense organs were lost and the muscular system reduced. The digestive system was greatly simplified and all accessory organs of reproduction were lost.

The argument is not wholly convincing. It is not easy to prove that the sequence, if it is real, did not run the other way, from Coelenterata to Turbellaria. When animals become ' degenerate ' they usually trail some clouds of their former glory. Barnacles remain Crustacea ; tapeworms still retain platyhelminth features ; the meanest bivalve is still undeniably a mollusc. But in the supposed degeneration of the Coelenterates every single distinguishing turbellarian feature has by hypothesis been removed. That is indeed a possibility : it is a somewhat remote probability.

In one important respect I am in full agreement with Hadzi, though for rather different reasons. Of the three great classes of Cnidarian Coelenterates, the Hydrozoa, the Scyphozoa and the Anthozoa, it is the last of these, the sea-anemones, that is the most primitive.

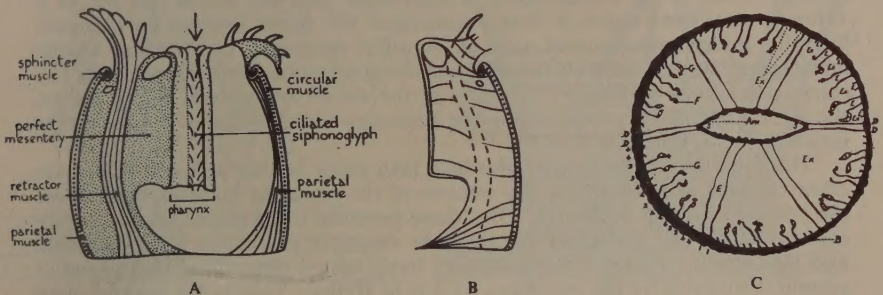
In Haeckel's day the polyp Hydra was taken to be a primitive animal. But today it is abundantly clear that Hydra is a degenerate representative of the class Hydrozoa, in which group the polyp is typically an immature stage on the way to the development of a Medusa. Analogy with the Trachyline medusae suggests that the final medusoid stage has been suppressed in Hydra. The evidence for this is well summarized by Hyman (1940) in her text-book, pp. 634–635. There is indeed some indication that Hydra may have re-acquired certain primitive features particularly in its musculo-epithelial system. But its position is clearly betrayed by its nematocysts.

Nematocysts, or stinging capsules, are characteristic of the Coelenterata. But the possession by Hydra of four distinct types closely resembling those of certain athecate hydrozoa, each specifically adapted to special functions, provides clear evidence of Hydra's relationship—and the secondary character of its simplicity.

Both the Hydrozoa and the Scyphozoa are in fact primarily Medusae ; and these jellyfish achieve great complexity in muscular and nervous organization

and in their specialized sense organs (Hertwig, O & R., 1878; Bozler, 1927; Horridge, 1953). In contrast, the Anthozoan polyps show no indication of ever having possessed a medusoid stage. Moreover, as the Hertwigs (1879) showed long ago, they not only possess no specialized sense organs, but their whole nervous organization is simpler. They are also simpler in those characteristic structures of the Cnidarian Coelenterates, the stinging cells. In both the Hydrozoa and the Scyphozoa nematocysts are contained in cells, the cnidoblasts, which possess specialized structures for their excitation and discharge; the cnidocil and contractile fibres. The cnidoblasts of the Anthozoa lack differentiated cnidocils. All they possess are functional cilia (Weill, 1934; Pantin, 1942).

I shall return later to the simplicity of sea-anemone organization. Nevertheless the Anthozoa do show important specialized features, compared with a simple polyp like Hydra. These are the mesenteries, the pharynx and a special-



TEXT-FIG. 1.

A. Vertical section through *Metridium senile* to show retractor musculature, pharynx and siphonoglyph.
B. Radial face of 'perfect' mesentery.
C. Transverse section of *Calliactis parasitica*, showing radial pattern of mesenteries, and bilateral pattern of pharynx and siphonoglyph.
A and B from Batham and Pantin, 1950 *a* and C from Stephenson, 1926, Fig. 29 by permission of the publishers.

ized part of the pharynx, the siphonoglyph (Text-fig. 1). The mesenteries are usually muscular. They are curtain-like folds of endoderm arranged in cycles, which, in the Actiniaria or true sea-anemones have a striking hexameral radial symmetry (Text-fig. 1C). In some other orders, notably in the primitive *Cerianthus*, the pattern of the mesenteries is not truly radial, for they are more weakly developed as we pass from one end of the mouth to the other. The Anthozoan pharynx is a flattened sleeve-like tube. Typically at one or at both edges of this collapsed tube is a flagellated siphonoglyph (Text-fig. 1A), which carries sea-water at low pressure to inflate the gastral cavity (Batham & Pantin, 1950 *a*).

The pharynx imposes an element of bilateral symmetry on the radial symmetry of the animal. This, and the division of the gut into regular compartments by the mesenteries along the line of the drawn-out pharynx, was held by Sedgwick (1884) to be a forerunner of the bilateral symmetry and even of the segmentation along the blastopore of the higher Metozoa. On the other hand Hadzi (1953) more recently considers that the 'sessile and therefore, radially symmetric cnidaria must be derived from bilaterally symmetric animals which led a free life and possessed free locomotion', and that the Anthozoa, which exhibit distinct traces of bilateral symmetry, are therefore the original group of

the Cnidaria from whence the others sprang. It is perhaps worth noting that the Actinaria are by no means devoid of free locomotion as part of their set of behaviour patterns (Batham & Pantin, 1950 *c*). Further, this ancient doctrine that sessile animals are radially symmetrical does not correspond very well with facts. Bivalve Molluscs, Brachiopods, Cirripedes, sedentary Polychaetes, Pterobranchiates and not a few Polyzoa are not radially symmetrical; whilst in this present argument one can scarcely be allowed to beg the question by basing the generalization, as Haeckel (1874) legitimately could, on the Coelenterates themselves.

The problem is a functional one, but perhaps it is not the best way to solve it by trying to imagine how hypothetical ancestors swam, crawled and sat. It seems better to consider what is the known function of the parts concerned. Sea-anemones are pre-eminently hydrostatic animals, in which movement and change of shape are produced by a muscular body-wall acting upon a contained volume of fluid. The gastral cavity is kept inflated with sea-water (Batham & Pantin, 1950*a*). The advantage of a sleeve-like pharynx which can act as a valve to retain sea water is clear. And since the sleeve necessarily collapses laterally under pressure, an axis of bi-radial symmetry can become almost inevitable. Nor is it difficult to see how natural selection would then favour the conversion of one or both of the edges of the sleeve into special ciliary tracts, the siphonoglyphs, for maintaining the necessary ' trickle-charge ' of sea-water into the gut to inflate it.

The function of the mesenteries falls into place in this scheme. They are often thought of primarily as the bearers of the retractor muscles which close the polyp by pulling in the disk. But these powerful longitudinal elements were evolved within the Anthozoa, for they are absent in primitives like *Gonactinia* and *Cerianthus*. In these the necessary longitudinal element of the muscular system is supplied by the ectoderm, as it is in Hydra. That is the natural place for it to be developed on mechanical grounds, except in those Anthozoa with a wide disk (Batham & Pantin, 1951). The primary muscular element of the Anthozoan mesenteries seems not to be the longitudinal muscle, but to be the transverse muscle sheets which are on the opposite face of the mesentery. The contraction of these opens the mouth, thereby not only admitting food but controlling the water-volume of the body (Batham & Pantin, 1950 *a*). According to the Hertwigs (1879) the mesenteries of *Cerianthus* seem only to bear transverse muscles.

If these inferences are correct, the bilateral element in the symmetry of the sea-anemones is the consequence of their hydrostatics. As speculation, this at least warns us that it is quite easy to conceive of the origin of bilateral symmetry in more than one way, and we must be chary of supposing that these features of the Anthozoa are indicative of a bilaterally symmetrical ancestor.

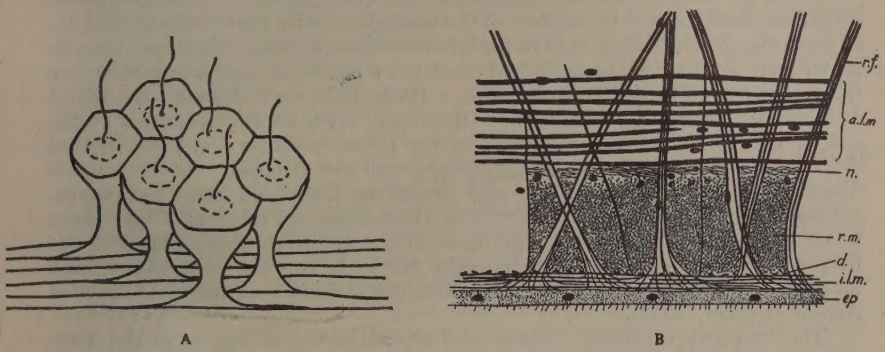
But whether we choose to derive Turbellaria from Coelenterates or, like Hadzi, Coelenterates from Turbellaria, all such speculations turn on one really important point: do the tissues of the Coelenterates resemble those of the Turbellarian worms or not? The answer generally encountered runs somewhat as follows. The body of a sea-anemone is built up of two epithelia, ectoderm and endoderm. Between these is collagen connective tissue which may contain amoebocytes. The body of a Turbellarian is built up of these same two epithelia, between which is connective tissue extensively invaded by cells, forming various tissues. It is true that the Coelenterate dermal layers often contain ' musculo-epithelial ' cells, and contain a simple nerve-net, instead of the deeper central nervous system of the higher animals. But are not musculo-epithelial cells and epithelial nerve-nets recorded as present in some Acoela and simple Rhabdocoels? Moreover both the mesogloea of Coelenterates and the mesenchyme of the Turbellaria and others are essentially a collagen connective tissue. and

though it is true that the Turbellarian mesenchyme is far richer in cells, is it not stated in text-books that mesogloea may sometimes contain in some degree amoebocytes, muscle, nerve cells and genital cells ; many of the elements in fact of a complex parenchyma ? In Hyman's (1940) view :—

> ' The radiate and bilateral phyla should no longer be distinguished on the basis of the alleged absence of a mesoderm in the former, and should not be offset against each other as diplobslatic and triploblastic groups respectively ; from a morphological point of view, shorn of phylogenetic theory, no actual difference exists between the construction of a sea-anemone and a planarian, as regards general body layers.'

Therefore whether we say that the Turbellarian grade is evolved from that of a sea-anemone or vice versa, is not the difference simply one of degree ?

The conclusion this question invites can be challenged. The answer depends upon how far the supposed Coelenterate features of the Turbellaria give more



Text-fig. 2

A. Anthozoan musculo-epithelial cells, to show relation of cell bodies to muscle fibres. (From Robson, 1957, by permission of the publishers).

B. Longitudinal section through wall of pharynx of *Hofstenia atroviridis* (Bock, 1923, Text-fig. 5 by permission of the publishers).

than a superficial resemblance, and upon how far Turbellarian or Coelenterate organization includes and depends upon characteristic structures not present in the other group : for such differences are more than a matter of degree and could make any possible evolutionary relationship distant.

Let us therefore compare the body wall of a sea-anemone and a planarian worm (Text-fig. 2 and Pl. 1). In both there is epithelial ectoderm and endoderm separated by a non-epithelial mass of fibrous collagen. The fibres are strongly marked in the Anthozoa. In the Turbellarian the mesenchyme contains muscle fibres which are individually wholly embedded in the collagen matrix. The muscles themselves are organized in depth, three-dimensionally as in a piece of beef. The main muscular system is below the ectoderm, not in ectoderm or endoderm (Text-fig. 2B).

In contrast the entire muscular system of the Anthozoa is in the ectoderm or the endoderm : I shall refer to its occasional relation to the mesogloea later. It is based upon a two-dimensional network of muscle fibres attached, by one surface only, to the outer surface layer of the mesogloea (Batham & Pantin, 1951 ; Robson, 1957 ; Grimstone, Horne, Pantin & Robson, 1958). This muscle sheet may become highly folded : but it remains two-dimensional. Only one surface is attached to the mesogloea ; the other is free within the epithelium and bears the cell-body (Pl. 1A and C).

In the simplest cases, as in the Anthozoan endoderm, the muscle fibres are musculo-epithelial cells. The outer epithelial surfaces of these are attached to muscle fibres by cytoplasmic strands between which is an extensive intercellular fluid (Robson, 1957) (Text-fig. 2A). This occurs even where, as in the tentacles, the cell-body of the muscle cell does not extend outwards to the epithelial surface.

In the intercellular space are found individual gland cells, nerve cells and amoebocytes ; below it the sheet of muscle fibres is attached to the surface layer of the mesogloea. Consequently the endoderm, and similarly the ectoderm, is stratified. There is some analogy here with the complex stratification of the body wall of the higher animals (cf. Hyman, 1940) : but it remains an analogy, for in Coelenterates the strata are typically but one cell deep and are comprised within the span of single cells which stretch between the epithelial surface and the muscle sheet.

When we compare the organization of the Coelenterate dermal layer, with its precise limitation at the surface of the mesogloea, with that of the epithelium of those simple Turbellaria said to contain musculo-epithelial cells, the difference is striking. In none of the described cases has a basement membrane been seen (Luther, 1912, on *Childia* and *Palmenia* ; Bock, 1923, on *Hofstenia* ; Steinbock & Reisinger, 1924, on *Prorhynchus* ; Reisinger, 1924, on *Rhynchoscolex*). One can of course look with confidence to the future discovery of some fibrous system to which muscle fibres of the body wall are attached : to act, muscle fibres must pull on something, and something must pull them to cause re-extension. But in the absence of evidence of a basement membrane we cannot be certain precisely where the inner limit of the epithelium lies. Moreover the frequency with which the epithelial cells are sunk into the parenchyma, and may become syncytial, increases the indefinite character of the epithelium in Acoela (Luther, 1912).

The ' musculo-epithelial ' fibres of Turbellaria themselves have not been critically stained, and whilst some are quite likely to be contractile fibres, the possibility that some are skeletal rather than contractile has not been eliminated. Drawings show the fibres forming both longitudinal and circular systems together within the same cell ; and they lie freely within the protoplasm without evident skeletal attachment (Luther, 1912). Such a system is not easy to interpret either in its mechanics or in its nervous control. It differs strikingly from the characteristic Coelenterate sheet of muscle fibres directly attached to an evident mesogloeal surface (cf. Pl. 1C). On the somewhat rare occasions in which Coelenterates possess both circular and longitudinal muscle fibres on the same surface, they do so by adhering rigidly to Coelenterate principles of construction : the dermal layer is doubled, one sheet above another, each with its own set of muscle fibres. Thus in the sub-umbrellar ectoderm of the hydromedusan *Neoturris* there is an outer ectodermal layer with a sheet of circular fibres, and below this another layer with a sheet of radial fibres (Krasinska, 1914). When we thus examine the muscle sheets of Coelenterates and the musculo-epithelial systems of the simpler Turbellaria, they seem to have little in common in their functional plan and at best illustrate that contractile fibres may be developed in many different kinds of tissue ; a fact that is not surprizing in view of the common occurrence of acto-myosin elements in cells (Pantin, 1956), and that is as likely to be an indication of convergence as of evolutionary relation.

In the Anthozoa, over much of the surface, the two-dimensional muscle network forms a simple sheet. Powerful muscles, as in the retractors, are obtained by folding this plane sheet of muscle fibres, which carries portions of the epithelial cytoplasm with it. In this way a substantial thickness of muscle is obtained, but in a different way from the three-dimensionally packed fibres of a powerful muscle of the Triploblastica (compare Pl. 1A and Text-fig. 2B).

It is well known that certain sea-anemone muscles such as the marginal sphincter which closes the disk of *Metridium* when the animal retracts, are embedded within the mesogloea. But the muscle fibres are not individually and completely embedded in it as are those of the Turbellaria or the Ctenophora. They are arranged round the periphery of tubes of epithelium complete with intercellular space (Pl, 1B). The muscle fibres are not arranged round a core of mesogloea as stated by Hyman (1940). The core contains protoplasm and nuclei, as the Hertwigs (1879) pointed out. It is, in fact, epithelial and these epithelial tubes continue into the superficial epithelium and are no more than folds of the two-dimensional musculo-epithelial system partly separated from the general epithelial surface. The muscle fibres of the Anthozoa are found in both ectoderm and endoderm, but never seem embedded individually in the mesogloea. This is also true of the Hydrozoa, and Scyphozoa. The principles of muscle construction are morphogenetically different from those of the mesodermal muscles of Turbellaria and the muscle systems of the higher animals.

The development of muscle in the mesenchyme of flatworms places these on quite a different plan of construction from that of Coelenterates. In all such soft-bodied animals an outer muscular body wall acts upon an inner skeleton which can be deformed or distorted. Two systems of muscle are primarily necessary, circular and longitudinal. In Coelenterates these are supplied by both the primary layers, ectoderm and endoderm, outside the gastral cavity. The deformable skeleton is either the fluid in the gastral cavity or the cells of the dermal layers. It is never a deformable mesogloea functionally comparable to the deformable mesenchyme of Turbellaria. In Coelenterates the mesogloea itself only provides a skeleton against which the muscle sheets act when it cannot undergo plastic deformation but is turgid and capable of elastic distortion, as in Medusae. The system is simple and effective. It involves both ectoderm and endoderm—which differ less than do these tissues in any other Metazoan. It is noteworthy that the simple sheets of muscle do not allow for the development of oblique muscles. Coelenterates do not twist the body and have no special musculature for flattening it.

The sytem in Turbellaria is different. The mesenchyme itself is here the deformable mass on which the musculature acts. Simple reciprocally acting muscle sheets in ectoderm and endoderm of such a animal would not be effective agents for complex movement of the whole body. Contraction of an external longitudinal muscle sheet would simply tend to make the animal become spherical: contraction of a circular endodermal body sheet would have little or no effect on the form and movement of the body, for it would be within the mesenchyme and could not exert direct pressure on it.

The new invention of the Turbellaria is the ability to develop muscle freely, and many fibres in depth, at any point in the mesenchyme. The primary antagonistic muscle layers are both developed below the limiting basement membrane of the mesenchyme—the sub-dermal muscular body-wall containing both circular and longitudinal layers, several fibres thick. Between these runs a layer of diagonal muscle fibres (Text-fig. 2B). Thus the prime effector system is external to the bulk of the interior deformable mesenchyme on which it acts, possessing thereby a different relation to the collagen connective tissue from that in a Coelenterate. In addition muscle fibres pass directly through the turbellarian mesenchyme from one side to the other. The animal is therefore able not only to extend and contract, but to twist and turn obliquely and to flatten in a manner impossible to a Coelenterate. In evolution the introduction of the mesenchymal muscle system was of first-rate importance. Some simple Turbellaria may possess musculo-epithelial cells as well—but these are of trivial mechanical importance in comparison with the mesenchymal system. And even when the type degenerates—as in Cestodes and Trematodes—it retains

the mesenchymal muscular machine. It does not lose it and develop musculo-epithelial sheets in its stead ; for as a mechanical solution of the problems besetting a soft-bodied animal the mesenchymal muscle system is simpler as well as more varied in what it can do. Evolution is conceivable by adding this important new principle of organization to the mesogloeal plan of a Coelenterate. That it should be lost in exchange for the Coelenterate plan seems improbable.

We may conclude first that whilst the ectoderm cells of Turbellaria may sometimes possess contractile fibres, their organization does not closely resemble the musculo-epithelial cells of Coelenterates, and that such a system may well have arisen independently from cytoplasmic contractile elements common to animal protoplasm ; secondly, that the evolution of the multi-fibred muscle freely penetrating the mesenchyme was an important and novel evolutionary step. It involves a morphogenetic principle for the development of musculature different from that seen in Coelenterates ; and it allowed a different and more generally effective mechanical system of muscular operation which, once gained, would be unlikely to be lost even in degeneracy.

Great as is the contrast between the muscle systems of a Coelenterate and a Turbellarian, the contrast of their nervous systems is even greater. Whilst some nervous elements may occur in the ectodermal epithelium of a typical Turbellarian, the mass of the nervous system is embedded in the mesenchyme. The nerve fibres are organized in a three-dimensional spongework. Even in the simple Acoela there is a small solid aggregation of nerve fibres to form a brain associated with anterior sense-organs. Indeed these animals have a head, which a Coelenterate has not ; and a brain with complex cellular connexions, which in the course of evolution is not to be lightly conjured out of nothing or lightly to be eliminated without trace (Pl. 2A).

The organization of the sea-anemone nervous system is different. As the Hertwigs (1879) showed, it is entirely epithelial. It is not a spongework, but consists of a two-dimensional network of nerve fibres from nerve-cells, and simple sensory cells. The nerve fibres are located in the intercellular space above the muscle sheet and below the epithelium. They are intra-epithelial (Pl. 3A and B).

Unlike the nervous system of the higher animals, the Coelenterate nerve-network is found in both endoderm and ectoderm, providing a complete sensory and motor system in each ; it is confined to these epithelia. In agreement with the Hertwigs (1879) all the work of my colleagues and myself shows no trace of nervous elements in the mesogloea (Pantin, 1952).

The nerve fibres themselves are in a very simple condition. The Anthozoan nerve-network resembles in several ways the network of fibres from a neuroblast tissue-culture from an embryonic chick (Hughes, 1953), except that instead of growing out in every direction it is two-dimensional. Histological features like the contacts between the fibres, and their terminal expansions, are like those of growing neurites. Moreover, the fibres of the nerve-network seem naked—at least so far as can be seen with the light microscope. There are no sheath cells such as are to be found in the vertebrata and insects (Edwards, Ruska & Harven, 1958), and molluscs (Geren & Schmidt, 1956).

A great deal has been written about the epithelial, or subepithelial, nerve-nets which are held to be a primitive character of the simplest Turbellaria (Bock, 1923, on *Hofstenia* amongst the Alloiocoela ; Steinbock, 1930, on *Nemertoderma* and *Tetraposthia* amongst the Acoela; An der Lan, 1936, on various Acoela). The best, and best illustrated account of the nervous system of these simple creatures is given by Westblad (1937) on *Nemertodema bathycola* Steinböck, which is a simple Rhabdocoel with affinities to the Acoela.

In all these animals there is a meshwork or plexus of nerve fibres outside the body wall musculature and below the epithelium. It is thus sub-epithelial in

position (Pl. 2C). It reaches a substantial thickness, because it is not built up of single nerve fibres but from cord-like bundles of nerve-fibres, forming a somewhat regular meshwork (Pl. 2B). Such an organized plexus of bundles of nerve fibres, below the epithelium, differs from the typical intra-epithelial nets of individual nerve fibres of Coelenterates (cf. Pl. 3A), though it may show some resemblance to the specialized nerve-rings of Hydromedusae.

Typically, the central nervous system of Turbellaria is embedded in the parenchyma. In the Acoela and some of the simpler Rhabdocoela and Alloiocoela it is concentrated round an otocyst. It has been suggested that in the simplest condition, as in *Hofstenia atrovindis* Bock and *Nemertoderma bathycola* Steinböck, the effective central nervous system was essentially the anterior thickened part of the sub-epithelial plexus and that the otocyst was only covered with neuropile and ganglion cells in the more advanced forms. But Westblad (1937) has shown beyond doubt that in *Nemertoderma*, one of the two held to be most primitive, the otocyst is covered with some neuropile and ganglion cells, even though of limited amount. He points out the essentially parenchymal position of this central nervous system.

Thus, as in the musculature, we find in the Turbellarian nervous system that an essential element is already embedded in the parenchyma. Unlike the two-dimensional networks of the Coelenterate nerve-net, it is organized as a spongework, in depth. Consideration of the ganglion-like aggregations of the nerve-net at the sense organs of Medusae suggests how the Coelenterate condition might be elaborated three-dimensionally to give ganglia of the Turbellarian sort. But these would still require to be sunk into mesenchyme.

Thus the sea-anemones provide a striking contrast to the Turbellaria in the epithelial and two-dimensional organization of both the muscular and nervous systems. In Turbellaria the main part of both systems is embedded in the mesenchyme, while there is no sound evidence that the Coelenterate mesogloea contains nerve-fibres ; the muscle fibres that become included in it are only carried in with extensions of the epithelia. The epithelial character of the muscle and the intra-epithelial character of the nerve-network is also clear in Hydra. From the beautiful work of Hadzi (1909) there also seems to be an intercellular system of spaces or vacuoles among which the nerve fibres run.

For some curious reason the figures in text-books of the dermal layers of Hydra have become progressively corrupt. Plate 4A is from Hadzi. The fibres of nerve cells and of the sensory cells are figured as running above the muscle fibre sheet, which is in contact with the mesogloea below. Plate 4B is from Schulze (1922). It is schematic. The nerve cells and sensory cells have been enlarged and shifted to the surface of the mesogloea ; and a fibre from one ectodermal sensory cell is allowed to slip through the mesogloea to the endoderm. The same block is used as an illustration to an article on the Coelenterata by Kukenthal (1924). The only new feature is that the schematic diagram is now '*nach präparaten*'. Plate 4C is from the first edition of a well-known text-book ; it shows an elaborate nervous system completely embedded in the mesogloea of Hydra, for the existence of which there is no evidence. Most well-known students' text-books today show the same corruption. The common impression that the Coelenterate mesogloea can be rich in differentiated tissue owes much to such erroneous figures.

It is true that both the mesogloea of Coelenterates and the mesenchyme of Turbellaria both contain collagen connective tissue. But the mesenchyme is rich in different kinds of cell, and in specialized organs. In contrast, except perhaps in the highly specialized Siphonophora, there are only two classes of cell which truly invade the mesogloea in Coelenterates, and thereby give it some character of a mesenchyme. Amoebocytes certainly occur in it—though they wander freely across the boundary into the epithelia as well. The only

other cells unequivocally to invade the mesogloea are the genital cells ; though this simple invasion by genital cells is very far from the complex development of genital organs always found in the parenchyma of the Acoela and other Turbellaria (Pl. 2D and Pl. 3C).

The differences between a Coelenterate and a Turbellarian are thus extensive and fundamental. They seem to me impossible to reconcile with a view that the Coelenterates are essentially degenerate Turbellaria. And if Turbellaria arose from Coelenterates we must insert a long evolutionary history of change in the principles of construction of its nervous, muscular and genital systems.

Strangely enough, there are better parallels elsewhere in the animal kingdom. Smith (1937) has shown the remarkable intra-epithelial character of the nervous system in the starfishes, both in the ectodermal sensory and the coelomic motor systems. Likewise Silen (1950) has shown a very striking parallel between this echinoderm condition and the ectodermal sensory and coelomic motor systems of the Hemichordata.

In Coelenterates there are often fistulae between the gut and the exterior as in the marginal pores of Scyphozoa and the cinclides and terminal pores of tentacles and base in the Anthozoa, and as in the gill slits and intestinal pores of Hemichordata. In Alcyonaria and in the Echinoderms we see a collagen connective tissue invaded by cells forming calcareous secretion. In the Anthozoa there is hydrostatic inflation of the gut from the exterior : the nearest parallel to which elsewhere in the animal kingdom is the hydrostatic inflation from the exterior of enterocoels in Echinoderms and Hemichordata. In passing, we may note in contrast that the coelom in the Annelid-Mollusc-Arthropod group is never inflated in this way, but secretes to the exterior.

There is one other curious point about the Echinoderms and Hemichordates. In both these the coelom differs strikingly from the coelom of the Annelid-Mollusc-Arthropod group in its relation to the genital cells. Here the coelom seems to be a genital cavity. But the coelomic cavity of the Echinoderms and Hemichordates is not a gonadial cavity. It is true that in these the genital cells are formed from the walls of the coelom, but they are passed into the mesenchyme to make their way to the surface where they acquire their own new genital cavity. That is not without a parallel in the formation of the gonads in *Branchiostoma*. To find a similar mesenchymal migration of the genital cells we must look to the Coelenterata.

I do not intend to erect a phylogenetic tree on these relations. All I wish to point out is that, for what they are worth, we can find parallels of morphology between Echinoderms or Hemichordates and Coelenterates which are at least as good as those between Coelenterates and Turbellarians. Comparisons of this sort, and even phylogenetic trees based on them, are useful because they bring before our minds important structural relations. They are dangerous when through their use of common terms they blurr distinctions. That is, I believe, the case when we say that the distinction between diploblastic organization of Coelenterates and triploblastic organization of the Turbellaria is only a matter of degree.

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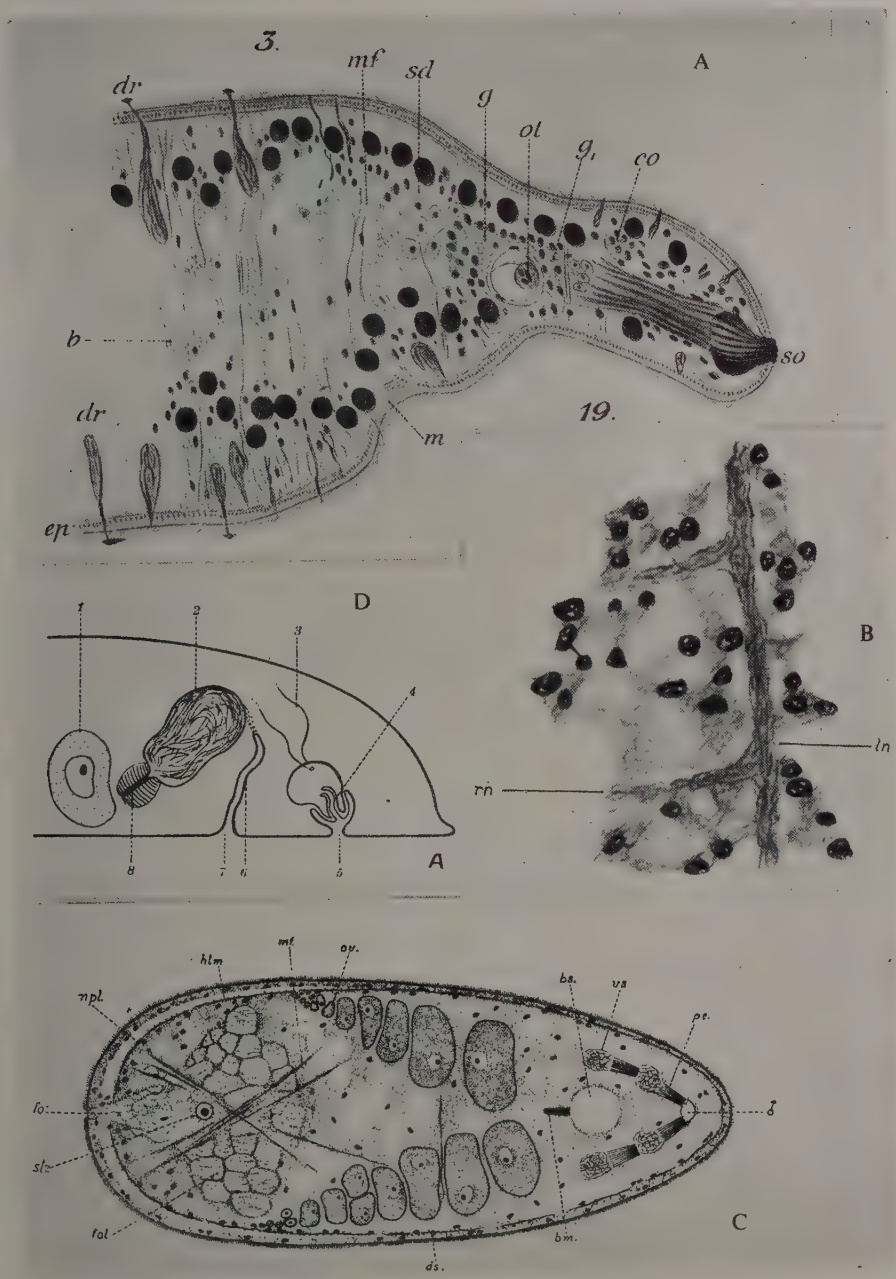
RICHARD PULTENEY, M.D., F.R.S. (1730-1801), AND HIS CORRESPONDENTS

By ROBERT H. JEFFERS, F.L.S.

Richard Pulteney, M.D., F.R.S. (1730–1801), author of a *General View of the Writings of Linnaeus*, (1781), and *Historical and Biographical Sketches of the Progress of Botany in England*, (1790), was a zealous promoter of Linnaean methods and nomenclature. He corresponded with most of the contemporary British naturalists. In a number of neatly tied bundles, Mr J. H. Robins generously presented to the Linnean Society in 1953 the correspondence of Pulteney and his wife Elizabeth. The collection has been arranged chronologically under the name of each of the 160 or so contributors, and also under each contributor. An alphabetically indexed manuscript register similarly arranged facilitates reference to it. It covers the period 1747 to 1801 inclusive, and links the correspondence of Richard Richardson, (1663–1741), Johann Jacob Dillenius, (1684–1747), John Ellis, (1705 ?–1776) and Linnaeus (1707–1778) with that of Sir James Edward Smith, (1759–1828) and William Swainson, (1789–1855), and is contemporaneous with that of Thomas Martyn, (1735–1825), William Curtis, (1746–1799) and John Coakley Lettsom, (1744–1815). These letters supply the basic material for the history of botany in England during the second half of the 18th century, when Linnaean nomenclature and classification gained their ascendancy, when the Linnaean Collections were brought to England, and the Linnean Society founded. The following notes are intended to indicate the main contributors and general nature of this correspondence.

Richard Pulteney was born at Mountsorrel, Leicestershire, on 18/19 February 1730, the only survivor of the 13 children of his parents, Samuel Pulteney, tailor, and Mary Tomlinson. At about 15 years of age he was apprenticed to Mr Harris, an apothecary of Loughborough, with whom he remained until 1752. By 1747, Pulteney was corresponding with *James Taylor*, and with *Thomas Harris*, son of the apothecary. Manuscript floras and botanical notes prepared by Pulteney between 1742 and 1749, now preserved in London and Leicester, clearly indicate his early attachment to natural history, in the study of which, his uncle, George Tomlinson, of Hathern, encouraged him. By 1749 he had discovered *Campanula patula* in Buddon Wood, and communicated the discovery to *George Deering, M.D.*, in Nottingham, and to *John Blackstone*, apothecary, in London. Pulteney's apprenticeship expired in March 1752, during which period a note concerning a patient was sent to him by *John Cheshire, M.D.*, of Leicester. A religious correspondence, begun in 1750 with *William Boss*, of Woodthorpe, was concluded in 1752 in which year Pulteney was, from April until October, in the service of Isaac Wylde, apothecary in Bridlesmithgate, Nottingham. There he met *John Gaunt*, a Quaker of Nottingham and Basford, and probably also *John Davison, M.D.*, a physician of Nottingham. Both corresponded with Pulteney who, in November 1752, established himself in practice as an apothecary in the Saturday Market, Leicester, where he remained until March 1765.

Professional duties introduced him to *John Fordyce, M.D.*, of Uppingham, and possibly also to *Maxwell Garthshore*, a surgeon there. Both became correspondents, and Garthshore, a life-long friend. *Ebenezer Latham, M.D.*, wrote from Derbyshire, and '*W.W.*' (probably William Watts, M.D., of Leicester) from Lichfield. *S. Judd*, apprentice-apothecary at Stamford, was added to the list in 1754, in which year Samuel Pulteney (1674–1754) died. Mrs Pulteney survived him, but her death is not alluded to in the surviving letters. Pulteney's uncle, *George Tomlinson*, (1696–1760) died at Hathern. Three interesting letters



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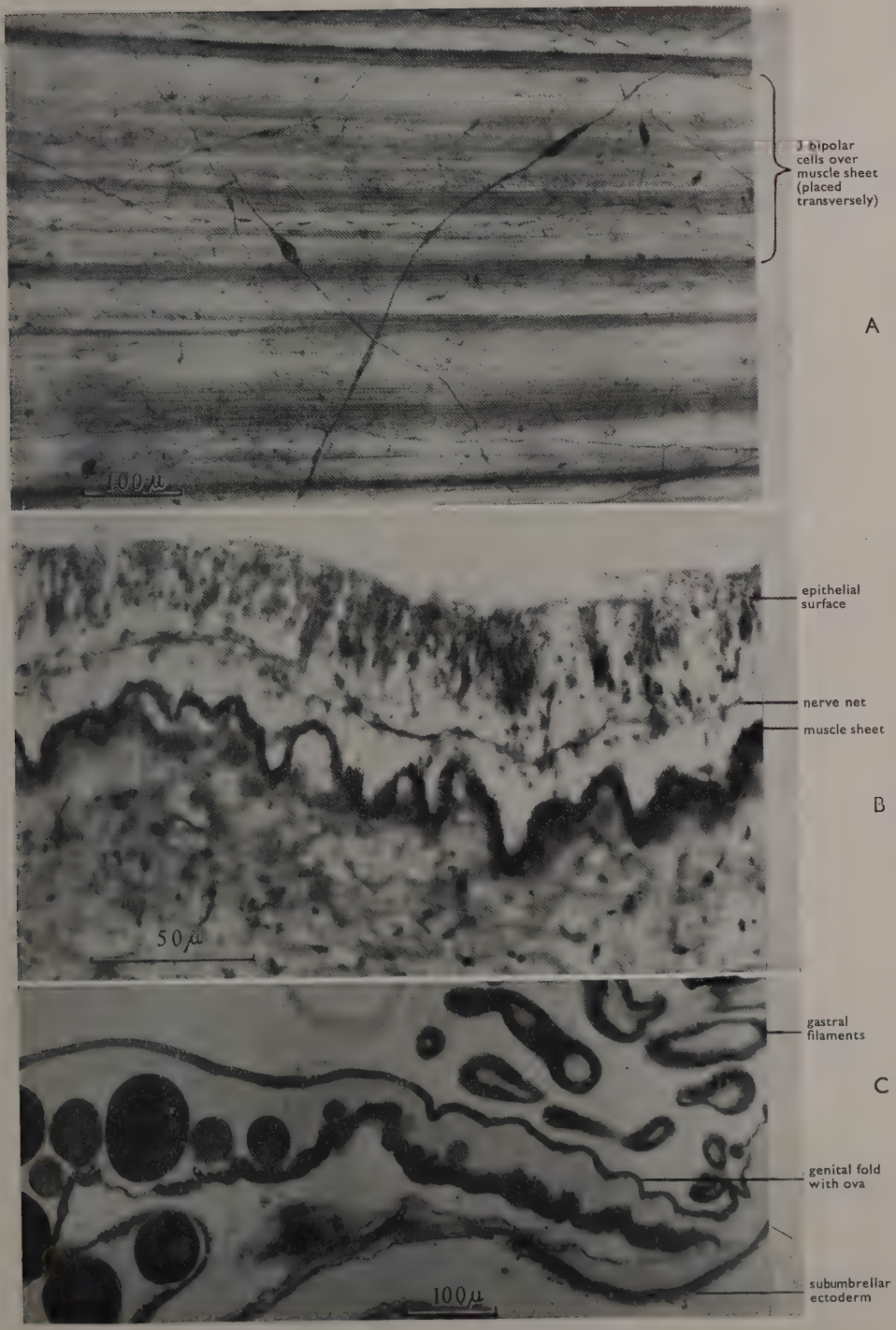

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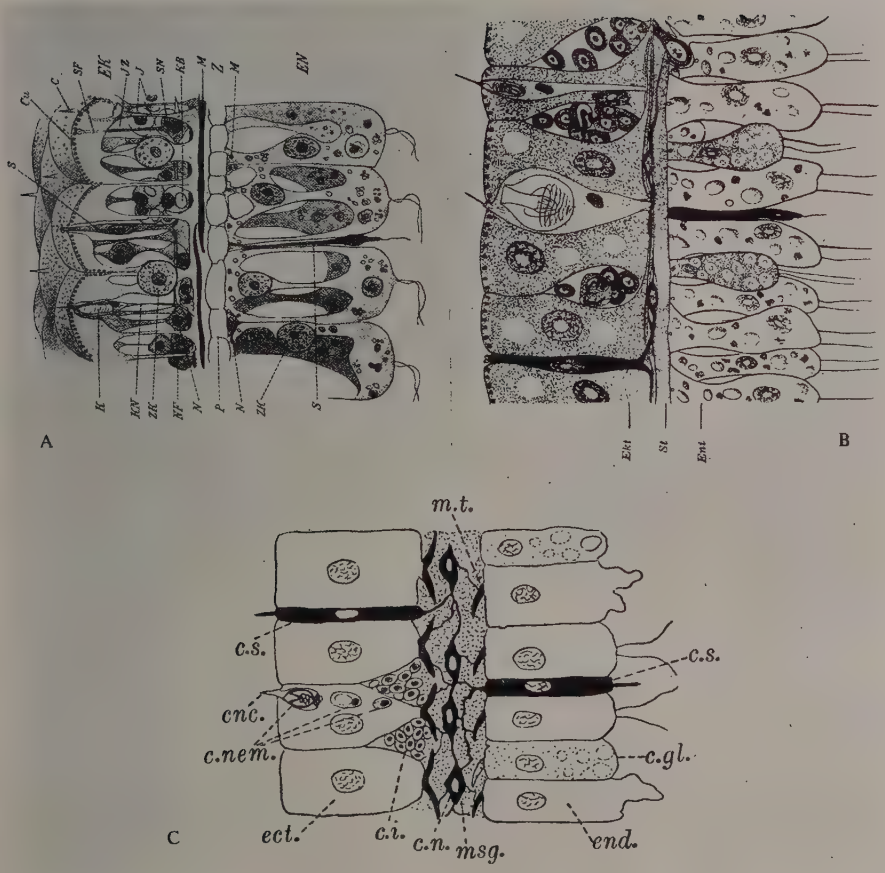

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By ROBERT H. JEFFERS, F.L.S.

Richard Pulteney, M.D., F.R.S. (1730–1801), author of a *General View of the Writings of Linnaeus*, (1781), and *Historical and Biographical Sketches of the Progress of Botany in England*, (1790), was a zealous promoter of Linnaean methods and nomenclature. He corresponded with most of the contemporary British naturalists. In a number of neatly tied bundles, Mr J. H. Robins generously presented to the Linnean Society in 1953 the correspondence of Pulteney and his wife Elizabeth. The collection has been arranged chronologically under the name of each of the 160 or so contributors, and also under each contributor. An alphabetically indexed manuscript register similarly arranged facilitates reference to it. It covers the period 1747 to 1801 inclusive, and links the correspondence of Richard Richardson, (1663–1741), Johann Jacob Dillenius, (1684–1747), John Ellis, (1705 ?–1776) and Linnaeus (1707–1778) with that of Sir James Edward Smith, (1759–1828) and William Swainson, (1789–1855), and is contemporaneous with that of Thomas Martyn, (1735–1825), William Curtis, (1746–1799) and John Coakley Lettsom, (1744–1815). These letters supply the basic material for the history of botany in England during the second half of the 18th century, when Linnaean nomenclature and classification gained their ascendancy, when the Linnaean Collections were brought to England, and the Linnean Society founded. The following notes are intended to indicate the main contributors and general nature of this correspondence.

Richard Pulteney was born at Mountsorrel, Leicestershire, on 18/19 February 1730, the only survivor of the 13 children of his parents, Samuel Pulteney, tailor, and Mary Tomlinson. At about 15 years of age he was apprenticed to Mr Harris, an apothecary of Loughborough, with whom he remained until 1752. By 1747, Pulteney was corresponding with *James Taylor*, and with *Thomas Harris*, son of the apothecary. Manuscript floras and botanical notes prepared by Pulteney between 1742 and 1749, now preserved in London and Leicester, clearly indicate his early attachment to natural history, in the study of which, his uncle, George Tomlinson, of Hathern, encouraged him. By 1749 he had discovered *Campanula patula* in Buddon Wood, and communicated the discovery to *George Deering, M.D.*, in Nottingham, and to *John Blackstone*, apothecary, in London. Pulteney's apprenticeship expired in March 1752, during which period a note concerning a patient was sent to him by *John Cheshire, M.D.*, of Leicester. A religious correspondence, begun in 1750 with *William Boss*, of Woodthorpe, was concluded in 1752 in which year Pulteney was, from April until October, in the service of Isaac Wylde, apothecary in Bridlesmithgate, Nottingham. There he met *John Gaunt*, a Quaker of Nottingham and Basford, and probably also *John Davison, M.D.*, a physician of Nottingham. Both corresponded with Pulteney who, in November 1752, established himself in practice as an apothecary in the Saturday Market, Leicester, where he remained until March 1765.

Professional duties introduced him to *John Fordyce, M.D.*, of Uppingham, and possibly also to *Maxwell Garthshore*, a surgeon there. Both became correspondents, and Garthshore, a life-long friend. *Ebenezer Latham, M.D.*, wrote from Derbyshire, and *' W.W.'* (probably William Watts, M.D., of Leicester) from Lichfield. *S. Judd*, apprentice-apothecary at Stamford, was added to the list in 1754, in which year Samuel Pulteney (1674–1754) died. Mrs Pulteney survived him, but her death is not alluded to in the surviving letters. Pulteney's uncle, *George Tomlinson*, (1696–1760) died at Hathern. Three interesting letters

from him on natural history subjects have been preserved. The long series of letters, dating from 1755, which represent Pulteney's correspondence with *William Watson, M.D., F.R.S.*, show that they corresponded before that year. Watson, then an apothecary in London, soon qualified as a physician, and practised as such. After the death of Samuel Pulteney, he was, to the son, a second father, a wise counsellor, and one of the architects of his career. He received the honour of Knighthood in the year preceding his death, and corresponded with Pulteney on medical, botanical and personal matters. To him, Pulteney sent his scientific papers, and Watson communicated them to the Royal Society, or sent them for publication in the *Gentleman's Magazine*. One such paper, Pulteney's '*A Catalogue of Plants Spontaneously growing about Loughborough and the adjacent villages*,' was published in the *Philosophical Transactions*. Watson apparently retained the original manuscript, as Jonas Dryander recorded its presence in 1797 in Sir Joseph Banks's Library, and catalogued it as ' MS. autogr. e Biblioth, W. Watson, Esq.'

Correspondence with *Nathaniel Cotton, M.D.*, physician and poet, occurred in 1757, and with the *Rev. John Aikin, D.D.*, then at Kibworth, Leicestershire, whence he removed in 1759 to Warrington as tutor in Warrington Academy. At Kibworth, Aikin was head of an academy at which two of Pulteney's correspondents were educated—James Taylor and *John Coltman*, and he was the father of a third—*John Aikin, M.D.* The long correspondence between Maxwell Garthshore and Pulteney had begun by 1758. Garthshore succeeded to Fordyce's practise at Uppingham in 1760, and to him John Aikin, jr., was apprenticed by his father. *George Baker, M.A., M.D.*, then practising at Stamford, and a friend of Garthshore, became a correspondent, but later settled in London, where he had a distinguished career, and eventually received a baronetcy.

By 1758, Pulteney corresponded with *William Hudson*, apothecary and botanist, in London, who, for a short time, was an assistant at the British Museum, of which William Watson, M.D., was a Trustee. Hudson, an infrequent correspondent, remained a life-long friend of Pulteney. During 1758 and 1759, Pulteney corresponded on botanical matters with *John Hill, M.D.*, then living in Pall Mall, London, and practising as a physician. He had begun the publication of the many works bearing his name, and was, at this time, preparing a British Flora. Hudson was similarly employed. To each of them Pulteney sent contributions respecting Leicestershire plants. Hill's Flora appeared in 1760, while that of Hudson, published in 1762, firmly established the Linnaean System in England.

An unpleasant professional circumstance arose about this time, which was sufficiently important for Pulteney to lodge a protest concerning it, with the result that his friends urged him to consider qualifying as a physician. On Watson's advice he added practise as a surgeon to that of an apothecary. This situation is reflected in the correspondence with William Watson, Rev. John Aikin, George Baker, Maxwell Garthshore, *John Sutton, M.D.*, of Leicester, and *Thomas Lee*, an attorney at Market Harborough. The discussion was very discreetly carried on for some time and during its progress Pulteney added to the number of his correspondents.

Thomas Bolton, of Warley Clough, was included in 1757. A naturalist, flower-painter, and plant collector, he supplied specimens of Yorkshire plants to the herbaria of Pulteney and *Thomas Arnold*, of Leicester, one of Pulteney's two pupils. Bolton's younger brother, James Bolton, of Halifax, enjoyed the patronage of the Earl of Gainsborough and the *Dowager Duchess of Portland*, and was the author of the work on fungi. Thomas Bolton's letters to Pulteney add to our knowledge of him, and his work on Yorkshire plants. He visited the Leverian Museum at Alkrington, and published an account of it, and inspected the Herbarium of William Harrison, in Manchester. Like Pulteney he had been

bred a botanist on the *Methodus* of Ray, and both were converts to the System of Linnaeus. Bolton complained of difficulties in securing copies of Linnaeus' works, and was a friend of *Thomas Knowlton*, who considered the Linnaean System could not last . Knowlton, at this time was gardener at Londesborough, but, many years earlier, had been gardener to James Sherard, at Eltham, under whose will, James Taylor, Pulteney's earliest correspondent, was a beneficiary. Bolton induced Knowlton to call on Pulteney at Leicester, but when at length he did so, business had taken Pulteney out of town. Knowlton left a note recording the visit. Pulteney lamented not meeting so distinguished a horticulturist and botanist, alluding to it in a letter to the *Rev. Thomas Martyn*, then Professor of Botany at Cambridge, with whom correspondence had begun in 1760. The letters received by Pulteney from Martyn were lent, after Pulteney's death, by Charles St Barbe, F.S.A., to the Rev. George Cornelius Gorham, by whom they were printed together with those from Pulteney to Martyn.

Pulteney's other pupil, *Timothy Bentley*, of Leicester, was the younger son of William Bentley, draper and banker of that town. Bentley went to Warrington Academy for a short time, where the Rev. John Aikin was one of his tutors. Afterwards he was a medical student in the University of Edinburgh, where Thomas Arnold joined him in the same capacity. Both thereby became correspondents of Pulteney. Arnold completed the medical course at Edinburgh, but Bentley left, and sought to further his medical studies in London. His father was disinclined to pay for further training, so Bentley became a brewer in Little Tower Hill. Writing from Edinburgh, both Bentley and Arnold furnished impressions of *John Hope, M.D.*, as a lecturer on botany. Arnold met at Edinburgh two fellow medical students—*William Withering, M.D.*, who became his immediate and life-long friend, and the author of a British Flora, and *John Rogerson, M.D.*, who was later Chief Physician to the Empress Catherine of Russia. On one occasion, Arnold and Withering returned in company to Edinburgh, and called, en route, on Thomas Bolton at Warley Clough. Arnold eventually contributed to the flora of Leicestershire.

Short letters are included in Pulteney's correspondence, written by *John Lewin*, of Leicester, to whose family he rendered professional services. Lewin was interested in British plants, some of his discoveries being duly attributed to him by Pulteney in the Catalogue of Leicestershire Plants he had published in the *Philosophical Transactions* in 1755. Lewin visited London in 1761, where he found *John Coltman* of Leicester, lying ill. He persuaded him to see John Fothergill, M.D., and then proceeded to Falmouth, en route to Lisbon and places round about, returning later to Leicester. Pulteney meanwhile had become a correspondent of the *Rev. John Lightfoot*, of Uxbridge, later the author of the '*Flora Scotica*.' Thus began a friendship lasting many years.

Pulteney now resolved to leave Leicester—his hesitancy in the matter having irked Baker, as Garthshore had already decided to give up practise at Uppingham and qualify as a physician. Pulteney was elected F.R.S. in 1762, though Watson, who assisted in the matter, urged that priority ought to be given to a medical qualification. Writing from Warrington, the Rev. John Aikin enlisted Pulteneys' aid in placing his son John Aikin as an apprentice-surgeon to Garthshore.

This was the situation in 1763, when Pulteney began correspondence with *John Hope, M.D.*, in Edinburgh. It continued until October 1786, and recorded the early history of the Botanic Garden which Hope established in Leith Walk, and Hope's work with *Rheum palmatum*, and *Asa fœtida*.

Early in 1764, *Lord Carbery* solicited Pulteney's professional attendance, and soon after this—in late February or early March—Pulteney quietly left Leicester. Together with Garthshore he took a chaise to Edinburgh, where they seem to have stayed with *James Garthshore, W.S.*, a cousin of Maxwell. The

two friends sat the necessary examinations at the University, and both graduated M.D. on the 8th May, 1764, each submitting a thesis. That of Pulteney, hurriedly prepared in under 12 months, was entitled '*De Cortice Peruviano officinalis Linnaei*,' and illustrated with an engraved plate drawn by *John Hawkins*, a surgeon at Dorchester, which Dr Hope supplied to Pulteney. The thesis was printed and published in Edinburgh in 1764, during Pulteney's short residence there. The graduation of Pulteney and Garthshore was the subject of a protest by some of the other students, who, admitting that the two candidates were eminently qualified professionally and academically for the degree, objected to their admission to it without residence. Among those who protested was *Arthur Lee*, who later graduated M.D., and became a Signatory to the Declaration of American Independence in 1776. He wrote a letter to Pulteney explaining his action. Arnold, who was still at the university, attended the meeting at which the protests were made, but did not actively oppose Pulteney, who was, nevertheless, piqued by the circumstance.

While in Edinburgh, Pulteney visited the site of the Botanic Garden in Leith Walk. He enjoyed hospitality, and was entertained by *Andrew Hunter, W.S.*, and his family. *Sir Archibald Dick, Bt*, of Prestonfield, paid civilities to him, as did also '*Dr R.R.*', who can hardly be other than Robert Ramsay, who had graduated M.D. at Edinburgh in 1757, subsequently becoming Professor of Natural History in the university, and a correspondent of Linnaeus. His successor in the professorship was the *Rev. John Walker*, upon whom Pulteney and Garthshore called at Moffat soon after their graduation, a circumstance which led to Walker sending lists of Scottish plants to Pulteney. The two friends visited Kirkcudbrightshire and Dumfriesshire, passed southwards through the Cumbrian mountains, and reached Leicester and Uppingham respectively. During his absence, Pulteney's practice in Leicester had been cared for by *John Aikin, jr.*, under the supervision of *Dr John Sutton*. Thereby, both were included among his correspondents. Pulteney arrived in Leicester by 1 June 1764, while Garthshore, having closed his Uppingham practice, joined his wife in London, where he commenced practice as a physician. Pulteney's first activity was an investigation, at Sheepey, of the genealogy of his family. On its completion, he went to London where, at a salon at Mrs Edward Montagu's he was acclaimed a kinsman by William Pulteney, Earl of Bath, to whom he was appointed domestic physician, with a prospect of immediate foreign travel. The Earl's death early in July completely frustrated this, so Pulteney was obliged to seek elsewhere for an opening as a physician. John Aikin now wound up Garthshore's affairs in Uppingham, after completing which he entered Edinburgh University as a medical student. Watson, Hope and other friends offered assistance in Pulteney's search for a post as physician, and eventually he succeeded Dr England at Blandford in Dorsetshire in 1765. This was probably John England who graduated M.D. at Edinburgh some years earlier. Pulteney's departure from Leicester in March 1765 was hurried. He went to London, qualified as an Extra Licentiate of the Royal College of Physicians in April, and was established in practice at Blandford by 13 May 1765. The successor in his business at Leicester was Robert Smith, a surgeon of Edinburgh.

A letter from the *Rev. John Harris*, of Sturminster Marshall, to George Baker, M.D., in London, disclosed that, at Baker's request, he had solicited assistance from apothecaries and medical men over a wide area in support of the new physician, so Pulteney's first task was to establish himself. The task was difficult, but successfully carried through.

In Dorsetshire, his first correspondents were *John Hawkins*, of Dorchester, the illustrator of his thesis, and *John Huxham, M.D.*, of Plymouth, who appreciated it.

From 1765 until 1789, Pulteney corresponded with the *Rev. James Stonhouse, M.A., D.Med.*, who, after having been a distinguished physician in Northampton, abandoned medicine for the Church. His decision to do so was helped by the Rev. Philip Doddridge, D.D., founder of the Northampton Academy, which in 1765 was under the *Rev. Caleb Ashworth, D.D.*, as the Daventry Academy. With him, Pulteney corresponded in 1766. Stonhouse resided at Bristol, where he was a neighbour of *Miss Hannah More*, to whom there is a draft letter by Pulteney appreciative of a poem she composed in his honour. Stonhouse held livings at Great and Little Cheverel, Wiltshire, under the patronage of the Earl of Radnor, so that some of his letters were addressed from Bristol, others from Wiltshire. They contain comments upon contemporary West Country medical men, more especially his friend, John Andrew, M.D., of Exeter, who met Linnaeus in Holland ; Henry Hele, M.D. of Salisbury, who attended the Earl in his last illness, and John Jacob, M.A., M.D., of Salisbury, a friend of *William Cuming, M.D.*, of Dorchester.

Pulteney's lengthy correspondence with *William Cuming* constitutes the bulkiest collection of letters in the Robins' collection. Cuming and Pulteney became life-long friends, and corresponded very frequently from 1766 onwards. Cuming had been a medical student at Edinburgh, but graduated at Rheims, later receiving an Hon. M.D. from Edinburgh. Archaeology was his recreation, and he was a friend and correspondent of John Coakley Lettsom, M.D., in London, John Hope, M.D., in Edinburgh, and George Cleghorn, M.D., in Dublin. His correspondence with Pulteney concerned medical matters, the literature of medicine, conchology and the History of Dorsetshire, a work compiled by the Rev. John Hutchins, M.A., and published posthumously mainly through the efforts of Cuming. In the second edition, Pulteney's second local flora appeared—'*A Catalogue of the Birds, Shells and more rare Plants of Dorset.*' after copies had been printed ' for the Author's use ' in 1799.

Another lengthy series of letters dating from 1766, was exchanged with *Henry Seymer* of Hanford, a keen naturalist, and painter of natural history subjects, particularly flowers, insects and birds. Being also a conchologist, he possessed a remarkably fine collection. His artistic abilities in natural history he shared with his son, *Henry Seymer, D.C.L.*, their skill in this work being, it was said, unexcelled. Bridget, elder daughter of Henry Seymer, the elder, married, as his second wife, Edmund Lambert of Boyton, Wilts, thus becoming stepmother of *Aylmer Bourke Lambert*, a Vice-Persident of the Linnean Society of London for many years. Henry Seymer frequently borrowed books from Pulteney and augmented his collection of shells by exchange and purchase. Among those who supplied him was *George Humphrey*, china-man, dealer in natural history, and one of the first Associates of the Linnean Society of London. A letter from him to Seymer, and another from Henry Seymer, D.C.L., to Pulteney, have been preserved. Soon after moving to Blandford, Pulteney seems to have been visited there by *John Bell*, hosier, of London, and a correspondent until 1770. After his death, *Jacob Bell*, his younger brother wrote appreciatively to Pulteney.

In 1767, the *Rev. Charles Pulteney*, Rector of Curry Mallet, Somersetshire, called on his friend Dr Cuming at Dorchester, whence he addressed a short letter to his namesake at Blandford. Thomas Arnold wrote during this year, and so, briefly, did the *Rev. Richard Farmer ,D.D.*, Master of Emmanuel College, Cambridge. A native of Leicester, Farmer assembled material for a history of the county, Pulteney supplying to him a list of Leicestershire plants, but upon assuming the Mastership of the College, he abandoned the work. His manuscripts were utilized later by *John Nichols*, almost the last of Pulteney's correspondents, who wrote and published a monumental history of Leicestershire, which included a list of plants supplied to him by Pulteney in place of the one

sent to Farmer. Dorset medical men included in Pulteney's correspondence were *Henry Nooth*, surgeon, of Sturminster Marshall, *John Mervin Nooth, M.D., F.R.S.*, his son, and *William Salkeld, M.A., B.Med.*, who practised for a short time in Dorchester, before moving to Fifehide Neville. John Mervin Nooth travelled on the Continent, served as a physician with the Forces in North America, and was present in London at the experiments in a heated room in which Sir Joseph Banks, Bt, Daniel Solander, M.D., and Charles Blagden, M.D. participated. Blagden sailed with Nooth to North America as a physician to the Forces. In a letter to Pulteney, Dr Cuming commended Nooth's account of the experiments in a heated room. That of Blagden was published in the *Philosophical Transactions*. He was later knighted. At an unknown date Nooth sent a plant from Ontario to Sir Joseph Banks, at whose house Garthshore and Pulteney were visitors. The friendship and correspondence of Pulteney with *Margaret Bentinck, Dowager Duchess of Portland* began in 1767. She was a conchologist, had a garden at Bulstrode, Buckinghamshire, and was a mutual friend of Seymer and Cuming, with whom, as with Pulteney, she exchanged shells. Daniel Solander, M.D. supervised her own collections, and after her death this collection was catalogued by the Rev. John Lightfoot, M.A., and sold by George Humphrey, together with the collection of birds the Duchess had bought from the widow of Thomas Bolton, of Warley Clough. Her letters to Pulteney included one written on her behalf by *Ralph Willett*, of Merly, Dorsetshire, and Soho, London. At Merly he had a valuable collection of books and prints, the latter including some drawings by Georg Dionysius Ehret, who, dying in 1770, appointed Willett the Executor of his Will. Willett wrote to Pulteney commenting on the very numerous drawings he found among Ehret's effects. Insects also interested the Duchess, this part of her collections being supervised by John Pattinson Yeats, while her shell collector at Weymouth was Mrs Le Coq, an amateur conchologist of ability. In a letter to the Duchess, Pulteney handsomely acknowledged his indebtedness to her for introducing him to the study of conchology.

As a struggling physician in 1767, Pulteney was little able to indulge in botanical field work. This was a sore trial, and he experienced at this time also some ill-health. *Peter Collinson* died in 1768. When at Leicester, Pulteney corresponded with him but none of this correspondence has survived. No new correspondents appeared until Willett wrote in 1771, and in 1772 *John Aikin, jr.*, now a surgeon at Warrington, resumed correspondence. Some time later he wrote from Great Yarmouth whither he removed from Warrington, practising first as a surgeon, but after graduating M.D. at Leyden he became a physician. His sister Anna Letitia Aikin married Rev. Rochemond Barbauld, and is referred to in the Aikin letters. John Aikin moved again to London, becoming associated there with Sir Richard Phillips, a publisher, and previously a newspaper proprietor in Leicester. The destruction of his offices there by fire was described to Pulteney by *John Coltman*, who by then had a collection of coins and was a friend of the Rev. Richard Gifford, the poet.

In 1771 Pulteney corresponded with the *Rev. Stephen Bolton, M.A., B.D.*, Rector of Stalbridge, who had observed a Transit of Venus, and in 1772 he corresponded first with the *Rev. Edward Oliver, M.A., D.D.*, then at Cambridge, but later Vicar of Greenhithe, and second with the *Rev. George Bingham, M.A., B.D.*, Rector of Pimperne. An aide-memoire in Pulteney's handwriting, bearing the date 1772, noted that *John Bassington*, nurseryman at Hoxton, then cultivated *Camellia japonica* and *Saxifraga crassula*. He was one of several nurserymen and gardeners in the vicinity of London to whom John Blake, of Parliament Street, Westminster, distributed the plants sent home by his son, John Bradby Blake, from Canton. During 1773, the health of John Fothergill, M.D., F.R.S., caused concern to his friends, and Dr William Cuming wrote to *William Cribb*

for information of it. Cribb wrote to Pulteney in the same year on a medical matter, being then a member of the Company of Surgeons practising in Holborn.

No new correspondents appeared until 1775 when *Jocilyn Pickard* became one, and on 22 November 1775 John Hill, M.D. died in Golden Square, London. An early correspondent of Pulteney, Hill is referred to elsewhere in Pulteney's correspondence. In 1773 Hill had been invested by the Swedish Ambassador in London as a Knight of the Order of Vasa, and on Monday 13 June 1774 'appeared at Court for the first time with the proper ensigns.' He had been appointed Master Gardener of Kensington Gardens in 1760, and possessed a well-stocked garden in Bayswater. Though he published a '*Hortus Kewensis*,' he never held a post at Kew. The Kensington post he owed to John Stuart, 3rd Earl of Bute, who had a garden and library in the closing years of his life at Highcliffe, near Christchurch, Hampshire. Pulteney visited them, and received from the Earl the gift of a copy of his '*Botanical Tables*'. Near Christchurch lived one of Pulteney's correspondents—*Edmund Bott*, Paymaster of Exchequer Bills, of Stourfield Farm, who introduced white clover into the county. Gustavus Brander, whose work on fossils is alluded to in Pulteney's correspondence, resided at the Old Priory, Christchurch.

John Warltire visited Pulteney at Blandford, and wrote to him in 1776. Warltire was a friend of the Rev. Joseph Priestley, LL.D., F.R.S., discoverer of oxygen, and repeated the work of Henry Cavendish, F.R.S. on electricity. His skill as a microscopist was utilized by Dr Cuming and Pulteney. Soon after its foundation in 1781, the Manchester Literary and Philosophical Society admitted Warltire an Hon. Member, while the Society's first President, Thomas Percival, M.D., F.R.S., is mentioned in Pulteney's correspondence by Sir William Watson, M.D., F.R.S., who visited him. Charles White, F.R.S., another member of the Society, was a surgeon in Manchester, under whom John Aikin, jr., served. The employees in the Royal Nursery at Kew House included in 1776, *Miss M. C. Goldsworthy*, sub-governess in Prince Ernest's house. She wrote to Pulteney soliciting support for the election of Joseph Planta as one of the Secretaries of the Royal Society. *Mrs Pulteney*, writing to *Miss Harriot Lister* at Beverley, Yorkshire, mentioned Princess Elizabeth, another of the Royal children.

Pulteney was on visiting terms with the *Rev. John Derby, M.A.*, of Fordingbridge, Hampshire, with whom he corresponded from 1777. Derby was a friend of Dr Cuming, and a member of a Dorsetshire family long associated with the Church. He contributed to the first edition in 1774 of Hutchins' '*History and Antiquities of Dorsetshire*.' When the 30th Regiment of the Line was quartered in Dorchester in 1777, its Chaplain, the *Rev. Edward Thomas, M.A., F.R.S.*, introduced himself to Dr Cuming, by whom he was introduced to Pulteney. Thomas visited him at Blandford and became a correspondent. His letters from Faversham refer to two naturalists—Edward Jacob, F.S.A., historian of Faversham, and John Latham, of Dartford. Both surgeons, Jacob's interest was in plants and fossils, that of Latham in ornithology.

The death of Linnaeus was announced prematurely in 1777 ; the event, of course, occurred on 10 January 1778, during which year Pulteney exchanged letters with *William Falconer, M.D., F.R.S.*, of Bath, and with *Peter Renaudet, M.D.*, a physician of Bristol, then visiting a patient at Wimborne. William Salkeld settled in Dorchester during the year, announcing to Dr Cuming his intention to practise medicine there.

The actual fact of Linnaeus's death was of peculiar concern to Pulteney, because he had been engaged, as opportunity offered, in preparing a manuscript whose publication was more than once urged upon him by Dr Cuming, who had been invited to read it over and suggest any necessary corrections. It dealt with

the life and work of Linnaeus, but Pulteney preferred to delay publication until after the death of Linnaeus, a course to which Dr Cuming assented.

Before the manuscript could be printed there were developments at Blandford. The Duchess of Portland introduced to Pulteney her protégé, *Mrs Sarah Sandford*, then living with her four sons at Lyme Regis. She corresponded with Pulteney from 1778, her letters forming a series in which those of three of her sons were included. These sons were the *Rev. Thomas Sandford, B.A.*, the *Rt Rev. Daniel Sandford, M.A., D.D.*, Bishop of Edinburgh, and *William Sandford*, a Special Pleader. All the sons were minors in 1778, their letters to Pulteney, and, in Daniel's case to Mrs Pulteney also, were all written during the early part of their respective lives. The fourth son, John Sandford, served in the Royal Navy and saw service in Newfoundland where he collected specimens of *Kalmia*, and in H.M.S. *Courageux*. Daniel had a leaning towards natural history and was a pupil of Pulteney who permitted him to read portions of his correspondence. These he marked : ' Read. D.S.' He attempted a translation of Linnaeus's works, visited William Aiton at Kew, and the Leverian Museum in London, but in the end he chose to enter the Church. Pulteney's disappointment in the loss of such a promising pupil was keen.

Mrs Sandford's correspondence contained letters exchanged between Pulteney and *Mrs Benjafield* of Blandford, *Mrs Ravaud* of Bath, and *Mr Jones*, a tutor to her sons.

Daniel Sandford's contemporaries at Oxford included William Garthshore, only son of Pulteney's friend, Maxwell Garthshore, and Matthew Wise, of Trinity College, descendant of Henry Wise, the partner of George London in the Brompton Park Nursery. The Professor of Botany at Oxford at this time was *John Sibthorp, M.A., D.Med., F.R.S.*, of whom, at Pulteney's request, Daniel Sandford enquired respecting the '*Pinax*' Library and Collections of Dr William Sherard. Disquieting rumours had been circulated but Pulteney was assured they were safe and intact at Oxford. Later he was able to visit Oxford for one day only. In a letter to the *Rev. Richard Relhan* at Cambridge, he described his pleasure at treading the Botanic Garden at Oxford, where the Bobarts once had trod, and his especial joy at seeing the Sherardian Collections, and particularly the '*Pinax*'. His one regret was that John Sibthorp had just left Oxford to begin his tour of Greece. One letter from Sibthorp to Pulteney has been preserved.

Mrs Sandford's correspondence included also a manuscript concerning Lord and Lady Mountcashel and their son.

For a short time Charles Blair, and his wife *Lady Mary Blair*, and their sons resided in Dorsetshire. A son, and probably Charles Blair himself, were patients of Pulteney, and Lady Mary became a correspondent. The family had just left Venice and when correspondence opened in 1778 were resident at the Chateau de Penthe, near Geneva. Lady Mary collected some items of natural history for Pulteney, and sent him a portrait of Haller.

Returning to Dorsetshire, Lady Mary visited Pulteney at Blandford. So also did the Dowager Duchess of Portland upon her journeys to and from Weymouth. William Hudson was a visitor, and so was the Rev. John Lightfoot. Thomas Lee, formerly of Market Harborough, visited Pulteney, and in 1785 *John Burton* was a visitor. In a letter to Pulteney he referred to the works of his father, John Burton, M.D. F.R.S., physician and antiquary of York.

John Coltman of Leicester resumed correspondence in 1779, and *Thomas Erle Drax* of Charborough, Dorsetshire, was an addition to the list. Together with Ralph Willett and Jocilyn Pickard he was a Governor of the Foundling Hospital, London, whose Treasurer, George Whatley, had corresponded with John Ellis, the naturalist.

During 1779, John Gifford, of Blandford, and a medical student at the Uni-

versity of Edinburgh, died at Tivoli, near Rome. His fellow student, Silas Neville M.D., and Pulteney were Executors of his will, under which Pulteney was also a beneficiary. This led him into correspondence with Garthshore, Hope and Cuming, and the estate was settled in 1780. While this matter was in progress Pulteney married *Miss Elizabeth Galton* in October 1779. Miss Galton belonged to two families long settled in Dorsetshire. The Galton family had a branch in Somersetshire, which gave rise to Samuel Galton, F.R.S, who as a result of a visit to Dorsetshire established kinship with Miss Galton. On her mother's side she descended from the Baskett family, among whom she had numerous relatives. These were augmented by marriages of the Basketts with the families of Galpine, of Dorsetshire, St Barbe, of Hampshire, and Foster of Lincolnshire. Her intimate friend and most voluminous correspondent was *Miss Harriot Lister* of Beverley, Yorkshire, whose letters reveal her to have been equally with Mrs Pulteney, cultured and well-read. She was also an artist, specially adept in pencilled landscape work, and she attended regularly the Assemblies at Scarborough. She visited friends in London. Her letters comment upon books she read, upon contemporary events, and give impressions of people she met. Mrs Pulteney's other extensive correspondent was distantly related to her by marriage. She was *Miss Eliza Purbeck*, one of four sisters who lived together in Southampton, and, for a short time, in Bath. Eliza and Jane Purbeck published novels anonymously, while Sarah Purbeck was the survivor of the quartette. In her letters Eliza Purbeck recorded contemporary events, and people she met, who included Mrs Sarah Sandford. While in Bath, the Purbecks had the company of *Miss Mary Foster*, a second cousin of Mrs Pulteney, with whom she resided for some years at Blandford, where she drew some of the plates for Pulteney's *Catalogue of the Birds, Shells and more rare Plants of Dorsetshire*. The Tomlinson, Pulteney and Galton families all bore arms, and after his marriage Pulteney used a seal bearing the arms of Pulteney impaling those of Galton. Mrs Pulteney was a collector of seals, and the doctor and his wife made their home at Langton, near Blandford. Pulteney's only new correspondent in 1780 was *Ingham Foster*, an ironmonger in London, with a fine cabinet of coins. The first of Pulteney's two books appeared in 1781—*A General View of the Life and Writings of Linnaeus*. It contained a biography of Linnaeus—the first in English—followed by English summaries of the contents of the *Amoenitates Academicas*. Next came ' Observations, tending to show the Utility of botanical Knowledge in Relation to Agriculture, and the feeding of Cattle : accompanied with a Translation of Linnaeus's *Pan Suecus*, accommodated to the English Plants, with reference to Authors, and to Figures of the Plants.' This part of the book had appeared some years earlier in the *Gentleman's Magazine* and was now reprinted ' with additional observations and some improvements in the general arrangement of the tables.' While the younger Linnaeus was in England, Pulteney sent to him the copy of the book now in the Linnaean Library. Writing later to the Rev. Richard Relhan, Pulteney expressed the view that the French translation, by Millin de Grandmaison, did not do him justice.

The year 1781 brought also new correspondents—*Mrs Elizabeth Warren* in London responded to an enquiry respecting the health of John Warltire ; the *Rev. J. .Howel* of Corfe announced an intended visit, and *Edmund Bott* of Stourfield Farm, and the *Rev. Henry Hall, M.A.*, of Child Okeford, Dorsetshire, each began their short series of letters. The arrival in London of the younger Linnaeus was a topic in the correspondence of Pulteney and Dr Cuming.

The publication of his book brought honours to Pulteney. *Thomas Naish* of Shaftesbury, and *T. Clothier*, a medical student in Edinburgh, assisted in promoting the election in 1782 of Pulteney as an Hon. Member of the Royal Medical Society of Edinburgh. In 1783 and 1784 *Edmund Rack* of Bath also

wrote. Rack was the founder and first secretary of the Bath Philosophical Society, of which Pulteney was admitted an Hon. Member. Rack was also founder and first secretary of the Bath and West of England Agricultural Society. Papers were contributed to each of these societies by William Sole, apothecary and surgeon, of The Crescent, Bath, though he died in Trim Street. Rack mentioned Sole's careful work on the British *Mints*. His ' Menthae Britannicae ' was illustrated by T. Robins, whom Henry Seymer recommended to John Ellis of Jamaica. Robins accompanied him thither, as an artist in natural history. Both were drowned in 1782 and Robins' collections lost.

The correspondence of Pulteney with the *Rev. Richard Relhan* of King's College, Cambridge, began in 1783. Another of Pulteney's correspondents, the *Rev. William Coxe* was a friend of *Mr and Mrs Henry William Portman* of Bryanston, near Blandford, and of Relhan. Yet another correspondent, the *Rev. Henry Hall* met Coxe at Bryanston, where Dr and Mrs Pulteney dined with the Portmans. Mr Portman cultivated exotic plants at Bryanston, and his gardener *Alexander Brown*, in 1789, sent a list to Pulteney of the more rare exotics which were being forwarded to William Hanbury at Kelmarsh, Northamptonshire. The list included *Camellia japonica*. In 1783 the Rev. Thomas Martyn was still Professor of Botany at Cambridge, but had handed to Relhan his manuscripts relating to British plants. These had been assembled since the publication of his *Plantae Cantabrigiensis*, and with them, and a zest for field work, Relhan embarked on the preparation of a flora of Cambridgeshire on the Linnaean System. He invited Pulteney's assistance, and their correspondence reveals the progress of the work. One of Relhan's letters enclosed a printed sheet :—the Proposals for the Publication of his *Flora Cantabrigiensis*, which appeared in Cambridge in 1785. The list of subscribers is an interesting one. It included Thomas Okes, M.A., M.D., a successor to the practice in Exeter of John Andrew, M.A., M.D., in 1770 ; William Salkeld (entered as John Salkeld) ; the Rev. John Frederick Browning, related by marriage to Mrs Pulteney ; William Curtis, of the London Botanic Garden ; James Bolton, of Halifax (younger brother of Thomas Bolton), who drew the plates illustrating the work ; and James Sowerby of London, who engraved them. Relhan published three supplements to this Flora, in one of which he recorded finding *Athamanta Libanotis* in the same station in which John Ray had recorded it, but which had been lost sight of since that time.

Thomas Arnold wrote again in 1784. When in Edinburgh he had married Elizabeth Graham, daughter of William Graham, a sadler there, and sister of James Graham, the quack doctor, and of William Graham, who after being a surgeon in the East Indies married in 1774 at Leicester the historian, Mrs Catherine Macaulay, widow of George Macaulay, M.D., and sister of John Sawbridge, Alderman of London. James and William Graham, and Mrs Macaulay, are all referred to in Pulteney's correspondence, and Arnold mentioned his sons, Thomas Graham Arnold and William Withering Arnold, both medical men. The younger Linnaeus died in 1783 ; in the summer of 1785 the Dowager Duchess of Portland passed away, and in 1786 Dr John Hope died. His death was followed, in 1787, by the deaths of William Cuming and Sir William Watson. Within this short period Pulteney was bereft of his closest friends and collaborators. For these serious losses there was some compensation. In 1784 *Dr James Edward Smith* purchased the Linnaean Collections, which arrived at his home in Paradise Row, Chelsea, during the autumn. There, during the autumn and winter of 1784–1785, Smith, Sir Joseph Banks and Jonas Dryander unpacked and checked them. Smith's correspondence with Pulteney began in 1786, continuing until 1797. The letters he received from Pulteney are in the Smithian Correspondence in the Society's Library, and have been calendared by Mr. Warren R. Dawson. Smith purchased works on natural

history, particularly foreign ones, for his friends, and rendered this service to Pulteney, who was elected a Fellow of the Linnean Society in 1790. He contributed some papers to the *Transactions*. In one letter to Pulteney reference is made by Smith to the genus *Pultenaea* which he erected in honour of his friend.

Fragments remain of a correspondence concerning neighbours of Pulteney—Capt (Sir) William Fraser, Bt, and Mrs (Lady) Fraser, and Mrs James Farquharson. There is also a solitary letter of 1788 from *Giles Russell*, younger brother of the Rev. Thomas Russell, reviver of the English ballad. The *Rev. Matthew Anstis*, Baptist Minister at Bridport, wrote in 1789, referring to *Rev. John Jones* of Loders, another correspondent of Pulteney. The *Rev. Hugh Worthington*, Pastor of Salter's Hall, London, wrote in the same year mentioning his father, the Rev. Hugh Worthington, many years Minister of the Great Meeting at Leicester, at the time Pulteney lived there. Pulteney's second book appeared in 1790—*Sketches of the Rise and Progress of Botany in England until the time of Linnaeus*—a work of biographical value which Thomas Cadell published in London in two volumes. He had been recommended to Pulteney as a publisher by Sir William Watson. An aide memoire in Pulteney's correspondence lists recipients of presentation copies, who included James Edward Smith and the Linnean Society. *Jonas Dryander's* manuscript comments on errors and omissions in the book are also preserved in the correspondence, together with a draft of Pulteney's reply in which a second edition is hinted at.

Thomas Bradley, M.D., and *James Buchan, M.D.*, in Edinburgh, jointly announced to Pulteney in 1790 his election to Hon. Membership of the Medical and Chirugical Society of Edinburgh. Bradley was originally a Worcestershire schoolmaster, but practised as a physician in London ; James Buchan practised in Edinburgh until 1835.

As a Fellow of the Linnean Society, Pulteney received notices of its meetings under the hands of two of its secretaries—*Thomas Marsham* and *Alexander Macleay*, his successor. These have been preserved together with a printed invitation from the President of the Royal Society (Sir Joseph Banks, Bt).

In 1791 *John White, jr*, a surgeon of Shaftesbury, of which town he was afterwards Mayor, wrote to Pulteney and in 1792 *John Ewart, M.D.*, wrote from Bath, mentioning his friend and fellow student at Edinburgh, Dr Addie. Ewart died some years later in Madras. *Joseph Staines*, a surgeon at Wareham where he became ' a considerable burgess ', wrote to Pulteney in 1792, and among Dr Garthshore's letters is a fragment from *John Rogerson, M.D.*, of St Petersburg, the friend and fellow-student at Edinburgh of William Withering and Thomas Arnold. In the same year, the *Rev. William Chafin, M.A.*, of Chettle, began a correspondence arising from a plant mentioned in the *Gentleman's Magazine*, but it was concerned mainly with ornithological matters. No clue exists as to when correspondence began between Pulteney and the *Rev. Thomas Rackett*, who was a friend of *Charles Hatchett, Tiberio Cavallo* and William George Maton, M.D. Rackett, Hatchett and Maton toured the West of England in 1792 and 1797. Of this group, Rackett was a conchologist and the editor of Pulteney's Dorset Catalogue ; Hatchett became a chemist and mineralogist ; Cavallo was distinguished as a natural philosopher, and Maton became a physician at Salisbury and Weymouth. Maton was also a botanist, and to him Pulteney bequeathed his papers and manuscripts. He edited the second edition of Pulteney's *Sketches*, contributing to it a biography of the author, and provided, as a frontispiece, a reproduction of the portrait of Pulteney, by the Dorset artist, Thomas Beach, which hangs in the Society's Hall. It was engraved by John Basire. Rackett's letters refer to another of his friends, Peter Woulfe, who at an earlier date was a correspondent of John Ellis, the zoophytologist.

A professional case in 1793, in which Maxwell Garthshore and Pulteney were

associated, led to *Sir Walter Farquhar, Bt, M.D.*, being consulted, who subsequently commended Pulteney for his conduct of it. The death in 1794 of the tenth Earl of Pembroke brought to Pulteney from *Barry Slatter* in London an account of the subsequent post mortem at which he was present. A Quaker, *John Rogers* of Godalming, wrote in support of a refugee French priest, and *Edward Hillman* of Winkton, Hants, also wrote. Some of Hillman's ornithological observations were recorded by Pulteney in his Dorset Catalogue.

Civilities extended to him induced the *Chevalier de Mouthault* to write to Pulteney in 1790, in which year an aide memoire in Pulteney's hand recorded a visit paid by him to *Samuel Lysons, F.R.S.*, the antiquary.

By the year 1796 over one hundred letters had apparently arrived for Pulteney from *Aylmer Bourke Lambert*, none of which have survived. Those remaining cover the period 1796 to 1800 and are brief, a few being written on his behalf by his wife, *Catherine Lambert*, and in one case by his amanuensis *J. Innis*. During this period Lambert recorded his acquisition of the collections of Johann Reinhold Forster, Archibald Menzies and Henry de Ponthieu. He referred to his visits to Pains Hill and elsewhere in quest of material for his *Description of the Genus Pinus*, and his *Description of the Genus Cinchona* appeared during this period. The sale of Lambert's Collections in 1842 included the plants of Forster, Menzies and de Ponthieu. A letter to Lambert written from Calcutta by *William Roxburgh, M.D.*, is included among Lambert's letters.

A new correspondent in 1797 was the bookseller *John Cuthell* of Holborn, and in 1799 the *Rev. John Tregonwell Lewis Napier* then aged 14 wrote a brief note. In the same year Pulteney received a letter from Noacolly, India, from *George Harris*, son of the Rev. John Harris who had assisted in establishing him in practice at Blandford.

Only two correspondents remain to be mentioned—*William Wright, M.D.*, of Edinburgh, distinguished for his botanical work in the West Indies, who promoted the election of Pulteney as a Fellow of the Royal Society of Edinburgh, and *John Nichols*, printer and antiquary, the author of the *History and Antiquities of the County of Leicester*.

While revising, in October 1801, the plate of the Melbury fossils which appeared in the second edition of Hutchins' *History and Antiquities of the County of Dorset*, Pulteney was seized with an indisposition from which he died at his home at Blandford on 13 October 1801. John Reid, M.D., of London, son of an old friend, attended him in place of Maxwell Garthshore who was unable to do so. The executors of his Will, were William George Maton, M.D. and Thomas Malkin of Cheapside, London, and he was buried in the churchyard at Shapwick, Dorset. His widow erected a memorial tablet in Blandford Parish Church, and sold his library in 1802, retaining, however, some of the books. William George Maton inherited his papers and manuscripts, and the Linnean Society of London received his herbarium and a sum of money, but part of the herbarium was sold in 1863. The remainder was incorporated in the Society's British herbarium. A few posthumous papers refer to *Charles St Barbe, jr*, who married Mary Foster, second cousin of Mrs Elizabeth Pulteney. Some letters from Lambert and Maton to Sir James Edward Smith, written after Pulteney's death and referring to him, are among the Smith Papers in the Society's Library. There, too, the manuscript of one of Pulteney's papers printed in the *Transactions*, and a portion of another, are also preserved.

Pulteney's place in British natural history is that of a pioneer author of local floras, a conchologist, and an historian of botany in Britain. He wrote the first biography in English of Linnaeus, and was a devoted and accurate student of his works, besides zealously supporting the Linnaean System. As Sir James Edward Smith wrote, his name will always be associated with that of Linnaeus.

THE GENETICS AND POLLINATION OF ANAGALLIS ARVENSIS SUBSP. ARVENSIS AND ANAGALLIS ARVENSIS SUBSP. FOEMINA

By E. M. Marsden-Jones, F.L.S., F.R.E.S.,
and the late F. E. Weiss, F.R.S., F.L.S.

Summary of the paper read on 2nd April 1959

In Britain there are two subspecies of *Anagallis arvensis* L. i.e. the subsp. *arvensis*.E.B. t. 1146 and *foemina* (Mill.) Schinz and Thell E.B. t. 1147.

The subsp. *arvensis* is a common plant, occurring in gardens, arable fields, by roadsides, on sand dunes, sometimes within a few feet of the sea.

Six naturally occurring colour varieties are known, var. *arvensis* (Grenadine[1] or Scarlet), var. *carnea* (Strawberry Pink), var. *pallida* (Cameo Pink), var. *lilacina* (Vinaceous-Purple (2) ?), var. *coerulea* (Deep Cadet Blue) and var. *vinacea* (Deep Purplish Vinaceous).

A. arvensis subsp. *foemina* is much more restricted in its habitat. In the eleventh edition of the London Catalogue it is recorded from 50 vice-counties, but we are inclined to doubt this, and think that var. *coerulea*, a colour variety of subsp. *arvensis*, probably caused confusion. When subsp. *foemina* occurs it seems to be present in great numbers. W. B. Turrill found two large populations of it growing with subsp. *arvensis* (Grenadine) in Oxfordshire, one at Kiddington, the other near Sturdy's Castle, both in the Woodstock district. R. C. Readett has informed us of two locations in Warwickshire, one at Wilmcote the other at Newbold-on-Stour. One of us has seen the plant in great quantity at the airfield at Hullavington, Wiltshire. In all these localities the plants were growing in calcareous soil, but we do not know if this is significant.

In a paper we gave before the Society on 21 April 1938, we indicated the essential differences between the two subspecies. These are summarized in the table on page 28.

From the table it will be seen that few characters are common to both subspecies. The smaller flowers, the colour of the flowers, but most of all the number of cells in the glands and staminal hairs, coupled with complete sterility in F_1 when crossed with colour varieties of subspecies *arvensis*, except var. *carnea*, provide stable diagnostic characters for the subspecies *foemina*.

Our experiments show that the different colour varieties of the subsp. *arvensis* are all fertile when crossed with one another, that Grenadine is the dominant colour and Deep Cadet Blue recessive. The colour variety Strawberry Pink is dominant to Cameo Pink and Deep Cadet Blue, and Cameo Pink is dominant to Deep Cadet Blue. This may indicate that the Grenadine colour is due to a number of genes, the loss of one or more causing the production of var. *carnea* and so on. It is also possible that the genes in question produce different degrees of acidity of the cell sap which operate on the anthocyanin pigments so that the flowers become blue, pink, scarlet etc.

A wide range of crosses was made between the various colour varieties. Mutations have occurred in four families, Vinaceous-Purple (2) which appeared twice, and Shrimp Pink, a dilute Strawberry Pink, which appeared in an F_3 family from Strawberry Pink × Grenadine. The F_2 plant selfed was Strawberry Pink and it gave 37 plants Strawberry Pink and 14 with Shrimp Pink flowers. Plants of Shrimp Pink were selfed for nine generations. Eight hundred and two plants were raised, but no segregation occurred.

[1] Ridgway R. *Color Standards and Color Nomenclature*, 1912, Washington, D.C.

	Subspecies *arvensis*	Subspecies *foemina* (Mill.) Schinz & Thell.
Leaves : lower	Broadly ovate.	Broadly ovate.
upper	Ovate or lanceolate	Usually lanceolate.
Pedicels	Considerably exceeding length of leaf.	Usually not exceeding or only slightly exceeding length of leaf.
Calyx	Not covering petals completely in unopened flower.	Completely covering petals in unopened flower.
Corolla	*arvensis* Upper surface Grenadine, lower surface Grenadine Pink.	
	var. *carnea* Schrank. Upper surface Strawberry Pink, lower surface Coral Pink.	
	var. *pallida* Hook. f. Upper and lower surfaces Cameo Pink.	
	var. *lilacina* Alefeld. Upper surface Vinaceous-Purple, (2) lower surface Light Vinaceous-Purple ?	Upper surface Grayish Violaceous Blue, lower surface Ramier Blue.
	var. *coerulea* Lüdi. Upper surface Deep Cadet Blue, lower surface Windsor Blue.	
	var. *vinacea* Marsden-Jones. Upper surface Deep Purplish Vinaceous, lower surface Purplish Vinaceous.	
Segments of Corolla	Usually overlapping to about half their length.	Not overlapping.
Diameter	Up to 1·4 cm.	Up to 1·2 cm.
Petal length	Up to 7 mm.	Up to 6 mm.
Petal breadth	Up to 6 mm.	Up to 3·5 mm.
Petal shape	Broadly obovate.	Narrowly obovate.
Petal margin	Entirely or obscurely crenulate on different plants. Rarely denticulate or crenulate on the same plant.	Denticulate.
Glands	Very numerous, 3-celled.	Few, 4-celled.
Staminal hairs	5–8-celled.	11–12-celled.
Seed germination	21·8 days.	31·5 days.
Chromosomes	2n = 40.	2n = 40.
Sterility	Complete compatibility between the various colour varieties.	When crossed with subsp. *arvensis* sterile except when the colour variety is var. *carnea*.

Besides the dilute colour, plants with Shrimp Pink flowers had internodes of 43·1 per cent shorter than those of a normal plant. The flowers were also usually smaller than normal. The gene or genes controlling length of internodes and size of flowers, like those controlling the colour, have also been modified.

When Shrimp Pink was crossed with Deep Cadet Blue the diluting gene or genes produced a Deep Grayish Lavender, a dilute Deep Cadet Blue and recessive to it. The F_1 family from this cross was Strawberry Pink or Shrimp Pink when in the full colour. Seven small F_2 families were raised, the total progeny consisting of 15 Strawberry Pink, 1 Shrimp Pink, 5 Deep Cadet Blue and 2 Deep Grayish Lavender.

The gene or genes controlling the length of internodes and the smaller size of flowers have also been transmitted. In this case there was a reduction in length of internodes to 56·6 per cent of that of a normal plant.

An interesting plant appeared in an F_4 family derived from var. *vinacea*

and Grenadine, a natural cross that occurred at Sark where there was only one plant of var. *vinacea* growing with many plants of Grenadine. The plant produced branches of Grenadine, parti-coloured Deep Hyssop Violet an dGrenadine, and Deep Hyssop Violet flowers. It was protected and seed saved from the various branches with the following result. Seed from Grenadine gave rise to a mixture of Grenadine, Deep Hyssop Violet, Deep Dull Bluish Violet (1), Deep Purplish Vinaceous and Dull Indian Purple. Seed from the other two branches gave Helvetia Blue but no Grenadine, the remaining colours being the same.

When a large number of crosses were made between the true subspecies it was found that only from the var. *carnea* was it possible to obtain a fertile F_1. When other colours were used only sterile F_1 families resulted. Even with var. *carnea* there was frequently impaired fertility or complete sterility in F_1 and subsequent generations. Only on three occasions did typical subsp. *foemina* reappear, although specimens that were true in all characters except corolla colour were sometimes noted.

We are unable to explain why the var. *carnea* of subsp. *arvensis* is able to produce a fertile hybrid when crossed with subsp. *foemina*. A further point of interest is that while the flowers of the F_1 plants are Strawberry Pink when crossed with the Deep Cadet Blue of subsp. *arvensis* it becomes slightly changed from Strawberry Pink to Chatenay Pink when crossed with the Grayish Violaceous Blue of subsp. *foemina*, thus showing a colour reaction. This instability of colour, possibly caused by the acidity of the cell sap, is still more in evidence in the F_2 and subsequent generations when a variety of shades of pink were produced, and, in addition, blue forms, some with the typical *foemina* colour, and some with different shades of blue. When a sterile F_1, obtained by crossing subsp. *arvensis* Grenadine with subsp. *foemina* Grayish Violaceous Blue, was treated with colchicine by Blakeslee a fertile shoot was produced and seed obtained. There was no segregation for colour of petals which were Grenadine on the upper surface, the lower surface being Jasper Pink instead of Grenadine Pink. There was somatic segregation, petals with blue fleckings, or quarter or half blue, and in 1943 a plant appeared with all the flowers the blue of subsp. *foemina*.

Pollination was a subject to which we paid special attention. The flowers on opening are adapted for cross-pollination. The stigma is then clear of the anthers, the style quite soon moves inwards and self-pollination takes place when the stigma is brought into contact with the anthers. Checks were made to test the amount of cross-pollination that takes place in the wild when two colour varieties were growing together. Of 26 sowings of natural seed that were made, there was no segregation in 23. Of the other three sowings, one produced three rogues, the others two rogues each. Five large populations of var. *arvensis* Grenadine growing with var. *foemina* were also examined. In two there were no hybrids ; of the other three one had six, one had two and one had one. Further experiments were carried out in an experimental ground where there were many colour varieties in close proximity. With one exception the number of ' rogues ' were under 10 per cent.

When there was ample opportunity for cross-pollination to take place very few hybrids were observed, and segregation was very partial. The explanation seems to be that a very small amount of foreign pollen was carried by an insect, or only very occasionally was a stigma in the right state to receive it. Thirty-two insects were observed visiting. Lepidoptera suborder Rhopalocera 2, Hymenoptera 10, Diptera 20.

From the results we are led to the conclusion that little cross-pollination takes place.

The research on which this paper is based has been aided by a Royal Society Government Grant.

THE FLORA OF A BREEDING AREA OF PINK-FOOTED GEESE IN CENTRAL ICELAND[1]

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(Communicated by the Botanical Secretary)

(With 1 Map.)

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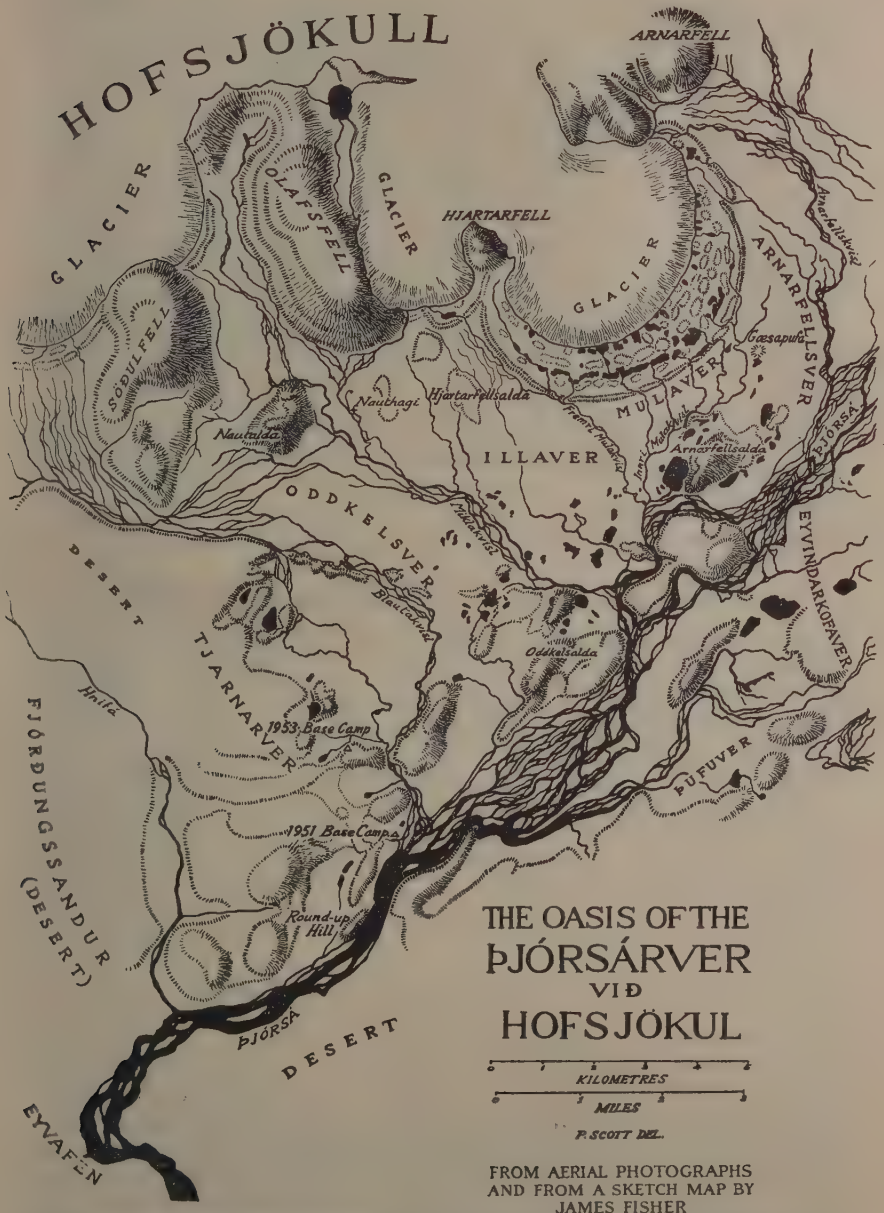
INTRODUCTION

THE largest known colony of breeding Pink-footed Geese (*Anser brachyrhynchus* Baillon) is at Thjórsárver vid Hofsjökul in Central Iceland. These geese and their habitat were studied in 1951 by the Severn Wildfowl Trust's First Expedition to Central Iceland (Scott, Fisher & Gudmundsson, 1953 ; Scott & Fisher, 1953), and in 1953 by the Wildfowl Trust's Second Expedition to Central Iceland, of which I was a member (Scott, Boyd & Sladen, 1955). In 1951 the expedition was in the breeding grounds from 28 June to 2 August, and in 1953 from 9 July to 7 August.

Thjórsárver vid Hofsjökul means ' the meadows of the River Thjórsá at the Hofsjökul Icecap '. This icecap in the centre of Iceland is surrounded by deserts of basalt and lava-sand, and the River Thjórsá originates at its southern and eastern margins. The meadows are enclosed by the terminal moraine of the icecap and exposed mountain slopes, and by the river, and are about 20 by 10 Km. in extent and at about 610m. (2000 ft.) above sea level. They consist of water-logged areas with a comparatively rich vegetation, dissected by streams supplying the river from the glacier, and scattered with pools, tarns and several hot springs. Interspersed are drier areas of tundra-heath dominated by *Empetrum* and *Salix*, and hills of moraine gravel exposed to the winds, whose shifting surfaces do not support a close vegetation.

The expeditions were principally concerned with a long-term population study of the Pink-footed Goose (Boyd, 1956). This is based on the ringing and recapturing of birds in their breeding areas in Iceland, Spitzbergen and Greenland, and in their wintering grounds, which are chiefly in Britain. The second expedition, of five British and four Icelandic men, drove flightless (moulting) adults and their young into nets on the tops of the gravelly hills, and put numbered rings on 9005 of the birds. From local recaptures it was estimated that the whole area at that time contained over 8,000 adults and over 10,000 young. The geese fed principally in the low wet parts and tundra-heath. Some indication of what they were eating was obtained from a collection of the crop contents of 10 goslings that were accidentally killed. Dr A. Melderis later identified the following species from this collection : *Equisetum variegatum*, *Galium pumilum*, *Juncus trifidus*, *Luzula spicata*, *Carex* sp. Sheep are annually brought in to graze from July until September, but during the study period of 1953, the sheep

[1] A preliminary report on the flora of the area was given at a General Meeting of the Linnean Society, on 6 May 1954 (*Proc. Linn. Soc. Lond.*, **166**, 16).



FROM AERIAL PHOTOGRAPHS AND FROM A SKETCH MAP BY JAMES FISHER

did not arrive. One effect of their absence was a luxuriant growth of *Angelica* on the moraine. In 1951 this plant was noted to have been severely grazed down.

On the first expedition, F. Gudmundsson identified 108 species of plants (Scott, Fisher & Gudmundsson, 1953 : 112–114), and his list was a valuable

guide for this report. Habitats are described here in simple terms, particularly because descriptions by Thoroddsen (1914), Gröntved (1942) and Steindórsson (1945) differ from, and overlap with, each other, and were therefore difficult to interpret during the short time in the field. During rounding-up of the geese, the whole area except mountain slopes below the icecap, was passed over at least twice, and in most places many times. This allowed an initial estimation of the distribution of the vascular plants to be made. During the last few days, a few places, then considered to be typical habitat representatives, were studied in detail. The habitats were chosen principally because they were also goose habitats—waterlogged areas where the geese fed most, drier mounds and heath banks where they fed and nested ; or because of unusual interest—the temporary nature of the gravelly hill surfaces (and because most of our time was spent on these hills, when ringing the geese).

A collection (411 sheets) was made to represent all the species, hybrids and varieties of vascular plants mentioned in this report for the British Museum (Natural History), London. Only those mosses and liverworts (101 sheets of specimens) repeatedly associated in the vascular plant communities were identified and deposited with the vascular plants in the museum.

The fungi in the upper respiratory tracts of the geese were studied, and cultures of fungi were made also from the ground where the birds were feeding (Sladen & Austwick, 1955). Notes on other animals of the area, particularly the vertebrates, are included in the expedition reports referred to above. Motion films were made of the expeditions.

Systematic List of Vascular Plants, Mosses and Liverworts

Notes are included on the habitat ranges, within the locality of Thjósárver vid Hofsjökul, of the species of vascular plants. A preliminary list was published in a general report of the expedition (Scott, Boyd & Sladen, 1955) ; here it is enlarged and corrected. Undoubtedly some late-flowering species could have been missed. Some specimens are referred to by the numbers attached to them in the British Museum collection. The nomenclature of the mosses follows Richards and Wallace (1950). These and the liverworts were named by Mr A. H. Norkett. Two pocket floras, Ostenfeld & Gröntved (1934), and Steindórsson (1948), were used in the field. All my identifications of vascular plants presented to the British Museum were later checked by Dr. A. Melderis. His authority is given for the *Cyperaceae*, *Caryophyllaceae*, *Alchemilla*, *Taraxacum* and *Hieracium*.

Most of the place-names are given on the map. The 1951 Base Camp is at Bolstadur. All references to Base Camp in the text concern the 1953 site.

(a) *Vascular Plants*

Ophioglossum vulgatum var. *polyphyllum* A.Br.

A new locality for Iceland, discovered by Dr Gudmundsson in 1951 (Scott, Fisher & Gudmundsson, 1953 : 114). He found it only along the banks of the hot springs at Nauthagi, where it grows in plenty. In spite of careful search, it was not seen during visits to the locality in the middle of July, 1953, but was conspicuous on 1 August. The specimens collected were unusually large, the leaves of one of the plants measuring 55 × 16 mm. The hot springs at Nauthagi are not sulphurous (solfataras). Some authors (Löve & Löve, 1948, p. 105 ; Hylander, 1953, p. 15, and 1955, p. 2) are of the opinion, that because of the peculiar ecological condition this species demands in Iceland (growing only in warm soil around sulfataras and hot springs), the Icelandic population should be referred to a new endemic variety, *islandicum* Löve & Löve.

Botrychium lunaria (L.) Sw.

Not uncommon on heath, heath banks, by streams and in mountain meadows. Occasionally on terraces on gravelly hills, and on sandy banks.

Cystopteris fragilis (L.) Bernh.

Found in two places only, at approximately 800 m. on damp rocky ledge. Jökulbrekka, and on the south-west crags of Arnarfell hid mikla.

Equisetum arvense L.

Rather abundant in a variety of habitats, chiefly in sandy, muddy or heathy places. Fertile spikes found only once, on the steep mountain meadow of Jökulbrekka. The procumbent form was the more common, and was found on bare mud edges of lakes, or in dry sandy or gravelly situations. The upright form was usually seen on heath banks among *Salix*.

Equisetum pratense Ehrh.

Found once (sterile stems) growing upright among fairly dense *Salix lanata* and *S. glauca*, at approximately 700 m., mountain meadow, Arnarfellsbrekka.

Equisetum palustre L.

Found once, growing upright in very wet moss-covered bank of a cold spring at the eastern foot of Nautalda.

Equisetum variegatum Schleich. ex Weber and Mohr

Common on gravelly hills and also sandy places. Procumbent.

Equisetum hyemale L.

Found twice, in damp gravelly place at about 800 m. along south-west slope of Ólafsfell, and in a dry situation on steep mountain meadow, Jökulbrekka.

Selaginella selaginoides (L.) Link

Found only once in damp ditch in *Empetrum-Salix* tundra, but probably overlooked elsewhere.

Potamogeton alpinus Balb.

In two small shallow ponds very near, but not connected with the hot springs at Nauthagi.

Anthoxanthum alpinum A. & D. Löve (*A. odoratum* s. Stéfansson, pro parte)

Found in only one area up steep mountain meadow, Jökulbrekka, where it was common.

Alopecurus aequalis Sobol.

Once found on wet moss by edge of a spring near Base Camp. Possibly more widely distributed as not found in flower until 5 August.

Phleum alpinum L. (*P. commutatum* Gaud.)

Common among rich vegetation on banks of streams, heath banks and mountain meadows. Undersized specimens (panicles *c.* 10 mm.) were found in wet area fed by the hot springs at Nauthagi, and unusually lush specimens (panicle *c.* 41 mm.) on steep mountain meadow of Jökulbrekka.

Hierochloë odorata (L.) Beauv.

Not uncommon on heath banks and mountain meadows. Often associated with *Geranium sylvaticum* and *Salix*. Occasionally found in wet places (hot springs, Nauthagi) and sandy banks (Base Camp).

Milium effusum L.

A few plants found in one mountain meadow (700 m.), Arnarfellsbrekka, growing among tall *Salix lanata*. Gröntved (1942) does not record this plant from Central Iceland, though more recently (Steindórsson, 1948, p. 49) it has been found at Karlsdráttur.

Agrostis stolonifera L.

Common in wet places and along streams. Often procumbent and creeping along muddy margins of lakes. Not uncommon in drier situations on gravelly hills.

Calamagrostis stricta (Timm) Koel. (*C. neglecta* (Ehrh.) G., M. & Sch.)

Common in flat, wet places, and often growing in water at edge of lakes.

Deschampsia alpina (L.) Roem. & Schult.

Common in many situations, e.g. wet moss-covered places, sandy banks, heath banks and damp peaty ground.

Deschampsia flexuosa (L.) Trin.

Found only twice. Not uncommon up steep mountain meadow, Arnarfellsbrekka ; and scattered plants on heath bank near Base Camp. A late flowerer, and not seen until 4 August, two days before we left the area, so probably more widely distributed.

Trisetum spicatum (L.) Richt.

Widely distributed though never very common on heath, heath banks, mountain gravelly slopes and sandy banks. Specimens (No. 348) collected from moist rock-ledge, 800 m., Jökulbrekka, had unusually dense, dark and broad panicles.

Catabrosa aquatica (L.) Beauv.

Only at Base Camp where it was common. Usually procumbent and growing on wet, moss-covered places. Not found elsewhere, but probably more widely distributed. A late flowerer, not noticed until 5 August.

Poa glauca Vahl

Common on sparsely vegetated gravelly hills and sandy banks.

Poa alpina L.

Not uncommon on sandy banks, heath banks, mountain meadows and banks of streams. Rare on gravelly hills.

Poa alpina var. *vivipara* L.

More frequent than *P. alpina*. On sandy banks, and scattered on heath banks, heath, damp peaty ground and wet rocky ledges. Occasional on gravelly hills.

Poa pratensis subsp. *alpigena* (Fr.) Hiit.

Not uncommon scattered on heath and heath banks. Dominant in small fenced corral at Bólstadur where there were remains of horse-dung. Also dominant in another smaller patch of heathland south of Oddkelsalda.

Poa subcaerulea Sm.

Occasional, e.g. scattered plants in wet area fed by the hot springs at Nauthagi, and in ' tundra ' mounds associated with *Empetrum* and *Cassiope*.

Festuca rubra L.

Frequent and chiefly on sandy banks and gravelly hills, and also heath and heath banks. Often growing side by side with *F. rubra* var. *mutica*.

Festuca rubra var. *mutica* Hartm.

Appeared to be much commoner than *F. rubra*, especially in sparsely vegetated areas on sandy banks, gravelly hills, Also found in wet area fed by the hot springs at Nauthagi, and near Base Camp.

Festuca vivipara (L.) Sm.

Less common than *F. rubra* and in sandy places and gravelly hills.

Eriophorum scheuchzeri Hoppe

Abundant in boggy places. Non-flowering plants frequently found in some situations.

Eriophorum angustifolium Honck.

Common in boggy places, often in shallow water on edge of tarns. Non-flowering plants frequently found in some situations.

Kobresia myosuroides (Vill.) Fiori & Paol.

Common on heath and heath banks. Occasionally on gravelly hills.

Carex maritima Gunn.

Not uncommon in wet or dry sandy places, often at foot of gravelly hills. Easily overlooked.

Carex curta Gooden. (*C. canescens* auct.)

Rare and found with certainty only at hot springs, Nauthagi.

Carex lachenalii Schkuhr

The six sets of specimens collected are very variable. Occasionally found in wet places, also on damp rock ledge at Jökulbrekka.

Carex rariflora (Wahlenb.) Sm.

Very common in wet places and often dominant on moss in bogs near streams or tarns. Occasionally found on wet heath banks.

Carex rostrata Stokes

Fairly common in wet places and often growing in shallow water near edge of tarns. Dominant in some areas such as the hot springs, Nauthagi, the bog round Base Camp, Bólstadur, and Oddkelsver.

Carex saxatilis L.

Not uncommon, and usually in small dominant clumps on firm edge of small tarns ; the bog round Base Camp, Bólstadur, Hnifárver.

Carex nigra (L.) Reich. (*C. goodenowii* Gay)

Very common in wet places and on the edge of tarns, and streams.

Carex lyngbyei Hornem.

Not uncommon in wet places. Dominant in some areas at the hot springs, Nauthagi, and near Base Camp. Its yellow-green leaves are easy to see at a distance.

Carex bigelowii Torr. ex Schwein. (*C. rigida* Good.)

Very common on heath and heath banks ; often in wet places and on banks of streams. Also on gravelly mountain slopes, gravelly hills and sandy places.

Carex rufina Drej.

Found once in a conspicuous patch in flat, wet area not far from a stream near Base Camp.

Carex bigelowii × *nigra*

Fairly common and usually in company with parent species. Five sets of specimens collected from bog by Base Camp, west of Hnifárver, and near Bólstadur.

Carex lyngbyei × *nigra*

Fairly common and usually in company with parents. Six sets of specimens collected from Nauthagi, Base Camp, and near Bólstadur.

Carex bigelowii × *lyngbyei*

Two sets of specimens collected from Base Camp, and edge of River Miklakvisl north of Oddkelsalda.

Carex bigelowii × spec.

One set of specimens collected from near Base Camp.

Juncus arcticus ssp. *intermedius* Hyl.

Common in firm wet places, usually sides of rivers or on gravel of occasional-river beds.

Juncus trifidus L.

Common and usually on heath or heath banks. Often on gravelly hills and sides of streams.

Juncus triglumis L.

Not uncommon on bare wet peaty patches (sometimes on mud) not far from water. It is more conspicuous than *J. biglumis* when in flower, but it loses its attractive cream colour in fruit. It flowers later than *J. biglumis*.

Juncus biglumis L.

Common and in same habitat as *J. triglumis*. An inconspicuous and easily overlooked plant. One specimen found with stem 16 cm. long. Occasionally only one flower in the inflorescence.

Juncus articulatus L.

On flat, firm, moss-covered edge of stream, by the hot springs of Jökulkriki, Upper Miklakvisl, where the plant was almost procumbent and probably grazed by the Pink-footed Geese.

Juncus bufonius L.

Growing in same habitat and within a few yards of *J. articulatus* near the hot springs of Jökulkriki. The specimens collected on 27 July, some of which already had well-developed capsules, were so small that it was difficult to distinguish them from the surrounding moss. Inflorescences mostly one-flowered, though one plant had six flowers. Stem 4–16 mm. Gröntved (1942, p. 188) records *J. bufonius* from two other localities in Central Iceland.

Luzula spicata (L.) DC.

Commonly seen on gravelly hills, heath, heath banks, mountain meadows, sides of streams and gravelly mountain slopes. Also in wet places. Very variable is size, the range in height of specimens collected being from 3·5 to 36 cm.

Luzula arcuata Sw.

In same situations as *L. spicata* but much less common.

Luzula confusa (Hartm.) Lindeb.

Specimens were collected from Base Camp and a damp rock ledge, Jökulbrekka.

Luzula ? *multiflora* (Retz.) Lej.

Found only by the hot springs, Nauthagi. Dr Melderis considered the specimens too immature to separate with certainty from *L. campestris*. Gröntved (1942) states that no specimen of *L. campestris* (L.) DC., with stolons, has yet been recorded with certainly from Iceland.

Tofieldia pusilla (Michx.) Pers.

Fairly common, and usually in wetter places on heath, heath banks and banks of streams.

Gymnadenia albida (L.) Rich. (*Leucorchis albida* (L.) E. Mey.)

Found in one place in steep mountain meadow between Jökulbrekka and Arnarfell hid mikla, where there were many plants.

Coeloglossum viride (L.) Hartm.

Common along the moraine (Arnarfellsmúlar) and the mountain meadows below Ólafsfell, Arnarfellsbrekka and Jökulbrekka. Occasionally seen elsewhere on heath banks or banks of streams (Nautalda, Tjarnarver).

Salix glauca L.

Very common on heath, mountain meadows, sandy and heath banks. Com-

mon on gravelly hills and wet places. A very variable plant and not always easy to distinguish from *S. lanata*. Growth normally only 15 cm. from ground but reaching 120 to 150 cm. at Arnarfellsbrekka.

Salix lanata L.

Very common and in same habitats as *S. glauca* from which it is not always easy to distinguish. Growth normally 15 cm. from ground but reaching 120 to 150 cm. at Arnarfellsbrekka.

Salix herbacea L.

Very common everywhere except in the wettest moss-covered bogs. It is abundant on heath and heath banks.

Salix phylicifolia L.

Less common than *S. glauca* and *S. lanata* and preferring wetter places. Often growing on wet moss, but also on heath and heath banks and not infrequently on gravelly hills.

Salix herbacea × *lanata*

Not uncommon near the parent species.

Betula nana L.

Found on heath in only a few places—Base Camp, near Bólstadur and Tjarnarver.

Rumex acetosa L.

Common on gravelly hills, sandy banks, heath banks and mountain slopes and meadows.

Oxyria digyna (L.) Hill

Common on gravelly mountain slopes and by streams (Ólafsfell, Jökulbrekka and Arnarfell) and all along the moraine Arnarfellsmúlar. Occasionally on gravelly hills or sandy banks. Also seen in the lava desert surrounding Thjórsarver.

Koenigia islandica L.

Very common on bare wet peaty patches on heath, heath banks and near tarns and streams. Less common on bare mud or among wet moss. Two distinct forms were found which are not mentioned in the literature. The typical form was with a single upright and very slender stem often tinged red. The other form (No. 384) found most often on bare mud or wet sand, was procumbent, branched and spreading with stouter stems.

Polygonum viviparum L.

Abundant on heath, heath banks and mountain meadows. Common in wet places and by streams. Occasional on gravelly hills and sandy banks.

Montia fontana L. (*M. lamprosperma* Chamisso)

Found only on moss edge of one of the hot springs at Nauthagi.

Cerastium cerastoides (L.) Britton

Common in wet places usually growing on moss carpets and often by streams or at the foot of heath banks. Less common in sandy places and damp gravelly places.

Cerastium alpinum L.

Very common on gravelly hills and mountain slopes, sandy banks, on heath and heath banks. Common in mountain meadows and by streams.

Cerastium alpinum var. *glabratum* Retz.

Found once on sparsely vegetated dry gravelly ground on moraine south of Hjartarfell.

Cerastium holosteoides Fr. (*C. caespitosum* Gilib.)

Found only near hot springs at Nauthagi where it was fairly common growing among moss and sedges, and on the edge of the streams.

Sagina intermedia Fenzl

Found only once on a wet bank near stream, Hnifáver. No. 144 from Base Camp is also probably of this species.

Sagina procumbens L.

Fairly common on heath banks and banks of streams.

Minuartia rubella (Wahlenb.) Hiern (glandular and glabrous forms)

Not uncommon on dry gravelly hills and sandy places.

Minuartia biflora (L.) Schinz. and Thell.

Not uncommon in wet places and stream banks.

Minuartia stricta (Sw.) Hiern

Once found on a bare damp patch on a tundra mound, Base Camp. This is further south than all records given by Gröntved (1942).

Arenaria norvegica Gunn.

Frequently seen on gravelly hills and sandy banks but not in large numbers. Occasionally in damp peaty places.

Lychnis alpina L. (*Viscaria alpina* (L.) G. Don)

Common on heath and heath banks where it prefers the bare peaty patches. Frequent on sandy banks and occasionally on gravelly hills. One plant (No. 180) with pure white flowers, but many intermediate shades of pink and red seen.

Silene maritima With.

Very common on gravelly hills and sandy banks. Also found on the bare gravelly banks of mountain streams at Jökulbrekka.

Silene acaulis (L.) Jacq.

Abundant in almost every situation, especially on gravelly hills, sandy banks, heath and heath banks. Sometimes found even in spongy wet moss. White-flowered plants seen on several occasions, and many shades of pink.

Ranunculus acris L.

Frequent on sheltered heath banks and mountain meadows. Often associated with *Geranium sylvaticum* when the two species make a fine display of colour.

Rannunculus pygmaeus Wahlenb.

Fairly common in damp gravelly places, crags and sides of streams up Ólafsfell and Jökulbrekka ; uncommon elsewhere—Base Camp, cold springs at Nautalda. Peduncles of specimens No. 355 found in fruit (Jökulbrekka), were unusually long (5·3–9·6 cm.). The height of these plants was 7–14 cm.

Ranunculus hyperboreus Rottb.

Fairly common and easily overlooked on spongy wet moss or on mud at side of tarns. Base Camp, hot springs at Nauthagi, Bólstadur, Oddkelsver.

Ranunculus confervoides (Fr.) Fr. (*R. trichophyllus* Chaix. var. *eradicatus* Laest.)

In a small pond in the moraine, Arnarfellsmúlar. Again found in small shallow pond near Bólstadur.

Thalictrum alpinum L.

Very common on heath, heath banks, mountain meadows and by streams.

Draba norvegica Gunn. (*D. rupestris* R. Br.)

Rather uncommon on heath and sandy banks, damp peaty ground ; also on mountain crags and ledges of Arnarfellsmúlar, Ólafsfell, Jökulbrekka. Also on sandy bank near Base Camp and on the roof of the Kofi at Bólstadur. Probably overlooked elsewhere, as it flowers early and was in seed when first found.

Cardamine pratensis L. coll.

Scattered plants common everywhere in wet places. Of specimen No. 94, Mr D. E. Allen writes '*C. polemonioides* Rouy, but with hybrid influence of another species'. No. 309 is an unusually small specimen with only one flower collected by Scott.

Cardamine bellidifolia L.

In a wet mossy place about 40 yards below a snow patch by a small stream, on west slope of Ólafsfell, *c.* 920m. This plant was first discovered in this locality by Dr Gudmundsson in 1951 (Scott, Fisher & Gudmundsson, 1953, p. 114). It was in flower and fruiting on 27 July in 1953.

Arabis alpina L.

Fairly frequent along the moraine of Arnarfellsmúlar, and on gravelly mountain slopes by streams and damp rock ledges of Ólafsfell, Jökulbrekka and Arnarfell. Also along sandy bank of River Thjórsá at 'Round-up Hill'. Rare elsewhere. Very variable in its growth.

Cardaminopsis petraea (L.) Hiit.

Very common on gravelly hills and sandy banks. Also common on gravelly mountain slopes. The glabrous form (*f. glabra* Blytt) appeared the commonest. One specimen (No. 380) with coarse hairs on the basal leaves was found on a damp rock ledge, Jökulbrekka.

Sedum acre L.

Non-flowering plants found in two places, near *Cystopteris fragilis* on damp rocky ledge of Jökulbrekka, and on sandy bank of R. Thjórsá just south of Bólstadur. No doubt more widespread, but easily overlooked when not in flower.

Sedum villosum L.

Not uncommon in wet places, bare wet peaty or gravelly patches, or by mountain streams. Often growing on spongy moss. A fine show near the hot springs near Jökulkriki.

Sedum rosea (L.) Scop.

Very common along the moraine where it flowers freely and attains an average height of 30 cm. Common by mountain streams and in mountain meadows. Also common on heath banks but blooms poorly in this situation, and often shows very stunted growth.

Saxifraga cespitosa L.

Fairly common on gravelly mountain slopes and crags and on gravelly hills, also by streams on bare ground of occasional-river beds, the bare moraine, and damp bare peaty places at the foot of heath banks. Very variable in its growth.

Saxifraga hypnoides subsp. *boreali-atlantica* Engl. & Irmsch.

Found once on a damp rock ledge near a stream up Jökulbrekka. It was not in flower.

Saxifraga cernua L.

Not uncommon on damp crags or gravelly places or by streams—Ólafsfell, Jökulbrekka, Arnarfell and moraine south of Hjartarfell. Rare elsewhere.

Saxifrage rivularis L.

Uncommon. In bare wet patches at foot of heath banks by mountain streams, damp rock ledges and in firm wet moss-covered places, cold springs at Nautalda, crags up Jökulbrekka, and Tjarnarver about ½ mile north of Base Camp.

Saxifraga oppositifolia L.

Common on gravelly hills and mountain slopes. Frequent on the gravel in the lava desert area around Thjórsárvar. Plants still in good flower on Olafsfell (about 800 m.) on 27 July, but elsewhere it was mostly over before our arrival on 8 July.

Saxifraga hirculus L.

Fairly common in firm wet moss-covered places or bare wet peaty patches. A most wonderful sight below Arnarfellsbrekka where it is dominant over about an acre. Here we found a few plants of the pale-yellow flowered form (No. 370).

Saxifraga nivalis L.

Less common than *S. tenuis*, but same situations.

Saxifraga tenuis (Wahlenb.) H. Sm.

Fairly common in bare wet peaty patches at foot of heath banks by mountain streams, damp rock ledges, and in firm wet moss-covered places. Very variable in size.

Saxifraga stellaris L.

Fairly common and in same situations as *S. rivularis*. Also grows commonly on wet spongy moss. Variable in size of flower and plant. Specimen No. 168 differs from the usual form in having a yellow patch at the base of the petals and the petals being sparingly dentate.

Parnassia palustris L.

Locally common on heath and heath banks south-west of Bólstadur and near Oddkelsalda.

Sibbaldia procumbens L.

Not uncommon on heath banks, along the moraine, and banks of streams —near Base Camp, cold springs at Nautalda etc. Also growing in turf of disused goose fold on Nautalda.

Potentilla palustris (L.) *Scop.* (*Comarum palustre* L.)

Found in two wet places among sedge, where it was common, hot springs at Nautalda and Base Camp. Also sparingly at the cold springs at Nautalda.

Potentilla crantzii (Crantz) G. Beck

Not uncommon on heath banks, mountain pastures, by streams, and along the moraine of Arnarfellsmúlar. Occasionally among rock debris of occasional-river beds.

Dryas octopetala L.

Common on heath, heath banks, gravelly hills and mountain slopes.

Alchemilla alpina L.

Found only in one place. One large plant in stone enclosure adjacent to the Kofiat, Bólstadur. It was not flowering.

Alchemilla filicaulis Buser

Specimens collected from two places, wet area fed by the hot springs, Nauthagi, and a bank of a cold spring at Nautalda.

Alchemilla wichurae (Buser) Stéfansson

Found only in steep mountain meadow (*c.* 700 m.) of Jökulbrekka.

Alchemilla glomerulans Buser

Rather uncommon on heath banks and banks of streams. One of the specimens (No. 226) was found on the bank surrounding the source of the main stream which ran past Base Camp.

Geranium sylvaticum L.

Fairly frequent on heath banks, mountain meadows and banks of streams. Sometimes in sparsely vegetated sandy areas. Often associated with *Ranunculus acris* and *Salix lanata* and *S. glauca* scrub.

Viola palustris L.

Rather uncommon on banks of streams and firm wet moss-covered places. Hot springs at Nauthagi, and hot springs near Jökulkriki.

Chamaenerion latifolium (L.) Sweet (*Epilobium latifolium* L.)

Common on gravelly and rocky beds of occasional-rivers. Not uncommon on sandy banks overlooking rivers and on flat bare rocky moraine. Blooms late and makes a fine show when in a mass.

Epilobium palustre L.

Found only at hot springs, Nauthagi, where it is common chiefly along edges of streams. In good bloom on 1 August.

Epilobium anagallidifolium Lam.

Common on banks of streams and other wet places—cold springs at Nautalda, Base Camp, etc.

Epilobium lactiflorum Hausskn.

Specimens collected from near the hot springs and in wet places, Upper Miklakvisl, Jökulkriki. Probably seen elsewhere. Gröntved (1942) considers it rare in the Central Highland, but records it from Arnarfell hid mikla.

Epilobium hornemanni Rchb.

Specimens collected from cold springs at Nautaldi from wet shady overhanging edge of one of the springs at its source. Specimens No. 321 from moraine at west end of Arnarfellsmúlar are probably of this species. Gröntved (1942) says there are only a few records of this species in the Central Highlands.

Hippuris vulgaris L.

Found only in two small ponds and on mud near hot springs at Nauthagi. This plant is rare in the Central Highlands.

Angelica archangelica subsp. *norvegica* (Rupr.) Nordh. (*Archangelica officinalis* s. Stéfansson)

Very common along the moraine Arnafellsmúlar where it flowers freely and grows to a height of up to 1 m. Fairly common elsewhere on heath banks, sides of streams and mountain meadows, but in these situations it is often only the leaves that are seen. This plant is undoubtedly reduced as a result of sheep grazing. No sheep were seen in 1953, and this probably accounts for lush growth on the moraine.

Pyrola minor L.

Not uncommon on heath banks, banks of streams and mountain meadows—Base Camp, bank of cold spring at Nautalda, bank near hot springs near Jökulkriki, and Arnarfellsbrekka.

Loiseleuria procumbens (L.) Desv.

Not uncommon on heath—Tjarnarver, west of Bólstadur, Oddkelsver near Oddkelsalda. Seen at its best on the heathy terraces up Nautalda. This plant

flowers early and could be overlooked later in season as its growth is similar to *Empetrum*.

Cassiope hypnoides (L.) D. Don

Very common on heath and heath banks. Common on mountain meadows and streams.

Vaccinium uliginosum L.

Locally abundant on heath and heath banks. Also found in mountain meadows.

Empetrum hermafroditum (Lange) Hagerup

Empetrum nigrum and not *E. hermafroditum* is listed for the area by Scott, Fisher & Gudmundsson (1953). *Empetrum* was abundant on heath and heath banks and common on mountain meadows, and often on gravelly hills where vegetation was consolidated in terraces. Only one voucher specimen was collected, and this proved to be *E. hermafroditum*. *E. hermafroditum* and *E. nigrum* were probably both present. The former is supposed to be more plentiful than the latter at high altitudes.

Armeria maritima (Mill.) Willd. (*A. vulgaris* Willd.)

Very common in sandy places and on gravelly hills. Common on heath, heath banks and gravelly mountain slopes. A few plants with white flowers were found ; one of these (No. 87) was found near Base Camp.

Gentianella tenella (Rottb.) H. Sm. (*Gentiana tenella* Rottb.)

Not uncommon on heath and heath banks at Base Camp, near Bólstadur, Tjarnarver, etc. Inconspicuous and easily overlooked.

Gentiana nivalis L.

Fairly common on heath banks and banks of streams at Base Camp, bank by stream at Bólstadur, cold springs at Nautalda, banks near hot springs near Jökulkriki, etc. Often growing near *Veronica fruticans* and *Gnaphalium supinum*.

Menyanthes trifoliata L.

Found only on the banks of the hot springs at Nautalda where the plants are bathed in steam. One fine specimen collected is 26 cm. high.

Thymus drucei Ronn. (*T. arcticus* (E. Dur.) Ronn.)

Very common on gravelly hills and sandy banks. Common on gravelly mountain slopes. This is a typical plant of dry gravelly ground and makes little patches of colour in an otherwise barren place.

Rhinanthus minor L.

Found only in firm wet ground near the hot springs at Nauthagi.

Bartsia alpina L.

Common on heath, heath banks, mountain pastures and banks of streams.

Euphrasia frigida Pugsl.

Specimens (No. 244) found later in same habitats as var. *pusilla* below and in seed were collected north of Oddkelsalda. *Euphrasia* is common everywhere and was always found with an unbranched stem.

Euphrasia frigida var. *pusilla* Pugsl.

Common on heath and heathy banks where it prefers damp bare patches on peaty ground.

Pedicularis flammea L.

Seen scattered everywhere on heath and heath banks. Also found in wetter situations such as the area fed by the hot springs at Nauthagi.

Veronica fruticans Jacq.

Rather uncommon on heath banks and banks of streams. It was flowering in profusion on banks by the stream at Bólstadur and on a bank south of the hot springs near Jökulkriki. Also found by the cold springs at Nautalda.

Veronica alpina L.

The only specimen (No. 72) in fruit, found at the cold springs of Nauthagi, fitted the type description having glabrous capsules and pilose margins to the capsules.

Veronica alpina var. *australis* Wahlenb. (*V. pumila* All.)

Fairly common on heath banks, banks of streams and in mountain meadows. The sepals are pilose on the back as well as on the margins, but the specimens Nos. 95 and 194 are too young for fruit.

Pinguicula vulgaris L.

Locally common on heath, less often on heath banks and banks of streams. In plenty on heath along River Thjórsá between Bólstadur and ' Round-up Hill ' ; also found at Base Camp, near Nautalda, and the heath slopes at the foot of Ólafsfell.

Littorella uniflora (L.) Aschers.

On wet mud not far from a stream. Found in only one place between Base Camp and Bólstadur. No doubt more widespread, but appears late in the season. The specimens collected were not even in bud when found on 6 August, the day before our departure. This is a new record from the Central Highlands. Specimens need to be collected from the same locality later in the season to confirm this record.

Galium verum L.

Found only in mountain meadows of Arnarfellsbrekka where not uncommon, but diffiult to find as not yet in full bloom on 4 August. For this reason probably missed elsewhere.

Galium pumilum subsp. *islandicum* Sterner (*G. pumilum* s. Stéfansson)

Common on gravelly hills and sandy banks. Also widespread on heath, heath banks and gravelly mountain slopes.

Erigeron uniflorus L.[1]

Not uncommon on heath banks and banks of streams. Also on damp rock ledges. At Base Camp, cold springs at Nautalda, Bólstadur, Jökulbrekka. Grönvtved considers *E. uniflorus* much rarer than *E. boreale* in Iceland, but this does not appear to be so in this locality.

Erigeron cf. *boreale* (Vierh.) Simm.[1]

One set of specimens (No. 278) collected from a heath bank, ½ mile south of the Jökulkriki hot springs might be *E. boreale*. The single flower-heads were larger than the *E. uniflorus* specimens seen ; height was 12½ to 15 cm. However, the small tubular pistillate flowers between the ray flowers and the disc flowers are absent, according to Dr A. Melderis who has examined the specimens.

Gnaphalium supinum L.

Common on heath banks, banks of streams and mountain meadows. Variable in size and numbers of flower heads. Specimens (No. 387) with single heads were collected from Bólstadur.

Gnaphalium norvegicum Gunn.

One flourishing clump found in mountain meadow at foot of Jökulbrekka. Not seen elsewhere.

Leontodon autumnalis var. *taraxaci* (L.) Hartm.

Two clusters found in the small fenced corral at Bólstadur. Not found elsewhere.

Taraxacum faeroëense Dahlst.

Found only in wet area fed by the hot springs, Nauthagi (No. 49). This may be a new record for the Central Highlands.

Taraxacum croceum Dahlst.

Fairly common on heath banks, sandy banks, banks of streams, and mountain meadows. The specimens were collected from a bank of a stream at the cold springs, Nautalda (No. 166), and from the steep mountain meadow, Jökulbrekka (No. 366).

Hieracium alpinum L.

Not uncommon on heath banks, in lush vegetation along the moraine and banks of streams—Base Camp, Arnarfellsbrekka, cold springs at Nautalda, Arnarfellsmúler, etc.

Hieracium microdon Dahlst.

Found once in the mountain meadow, Arnarfellsbrekka, where it was growing high among fairly dense scrub of *Salix lanata* and *S. glauca*.

Hieracium repandum Dahlst.

The same habitat as *H. alpinum*—Jökulbrekka, Arnarfellsmúler, Upper Miklakvisl etc.

[1] *E. uniflorus* versus *E. boreale*. I am indebted to Dr E. Einarsson for the following comments :—' In Iceland it is often very difficult to distinguish *E. uniflorus* from *E. boreale*, because specimens which habitually look most like *E. boreale* do not always have the tubular female discous flowers that characterize the species *E. boreale*. According to Böcher, Holmen and Jakobsen, 1957, p. 199, the same problem exists in Greenland. Their separation as two distinct species is therefore possibly a little doubtful '

(b) *Mosses. det* A. H. Norkett

Sphagnum teres (Schimp.) Åongstr.
Andreaea rupestris Hedw.
Pogonatum sexangulare Floerke
Polytrichum juniperinum Hedw.
P. commune Hedw.
Aongstroemia longipes (Sommerf.) Bruch & Schimp.
Blindia acuta (Hedw.) Bruch & Schimp.
Dichodontium pellucidum (Hedw.) Schimp.
Dicranoweissia crispula (Hedw.) Lindb.
Tortula ruralis (Hedw.) Crome.
Desmatodon latifolius (Hedw.) Bruch & Schimp.
Grimmia apocarpa Hedw.
G. funalis (Schwaeger.) Schimp.
Rhacomitrium canescens (Hedw.) Brid.
Splachnum vasculosum Hedw.
Leptobryum pyriforme (Hedw.) Wils.
Pohlia cruda Hedw.
P. drummondii (C. Muell.) Andrews
P. gracilis (Schleich.) Lindb.
P. ludwigii (Spreng.) Broth.
Mnium affine Bland.
M. punctatum Hedw.
M. cinclidioides Hüben.
Aulacomnium palustre (Hedw.) Schwaegr.
Paludella squarrosa (Hedw.) Brid.
Meesia uliginosa Hedw.
Bartramia ithyphylla Brid.
Conostomum tetragonum (Brid.) Lindb.
Philonotis fontana (Hedw.) Brid.
P. fontana var. *tomentella* (Mol.) Dixon
Drepanocladus aduncus (Hedw.) Warnst.
D. revolvens (Sm.) Warnst.
D. uncinatus (Hedw.) Warnst.
Acrocladium stramineum (Brid.) Richards & Wallace
A. giganteum (Schimp.) Richards & Wallace
Camptothecium nitens (Hedw.) Schimp.
Brachythecium reflexum (Starke) Bruch & Schimp.

(c) *Liverworts. det.* A. H. Norkett

Marchantia polymorpha L.
Fossombronia dumortieri (Hübret Genth.) Lindb.
Lophozia ventricosa (Dicks.) Dum.
L. alpestris (Schleich.) Evans
Cephalozia bicuspidata (L.) Dum.
Pleuroclada albescens (Hook.) Spruce
Blepharosoma trichophyllum (L.) Dum.
Scapania curta (Mart.) Dum.

Plant Communities of Selected Habitats

(1) *Bog where geese fed.*

(a) In the wettest part.

dominant :—

Philonotis fontana. This yellow-green moss is dominant on the edge of water, and shows an almost pure growth. *Drepanocladus uncinatus,* dominant further in, or mixed with *Philonotis.* This moss is also yellow-green. *Acrocladium stramineum* mixed with *Drepanocladus.*

abundant :—

Catabrosa aquatica. Calamagrostis stricta, leaves only. *Carex rariflora,* leaves only.

frequent :—

Eriophorum scheuchzeri, leaves only. *E. angustifolium,* leaves only. *Ranunculus hyperboreus.*

occasional :—

Alopecurus aequalis. Deschampsia alpina. Cardamine pratensis.

rare :—

Juncus arcticus ssp. *intermedius.*

(b) In a better drained and slightly higher place.

dominant :—

Drepanocladus uncinatus, dominant, and conspicuous throughout most of the area among the vascular plants.

abundant :—

Calamagrostis stricta. Carex rariflora. Salix herbacea, in the best drained areas.

frequent :—

Leptobryum pyriforme. Poa pratensis agg. *Eriophorum scheuchzeri*, leaves only. *E. angustifolium*, leaves only. *Carex bigelowii. C. nigra. Salix glauca. Polygonum viviparum.*

occasional :—

Mnium punctatum. Agrostis stolonifera. Festuca rubra var. *mutica. Salix lanata. Cardamine pratensis. Saxifraga hirculus. Euphrasia* sp.

Mosses collected from this habitat, in addition to those already mentioned, were *Sphagnum teres, Polytrichum commune, Aongstroemia longipes, Blindia acuta, Dichodontium pellucidum, Pohlia ludwigii, Aulacomnium palustre Paludella squarrosa.*

(2) *A well-drained mound and its slopes, in a boggy area.*

(a) A typical nest-site for the Pink-footed Goose.

abundant :—

Drepanocladus uncinatus. Carex bigelowii. Polygonum viviparum. Thalictrum alpinum.

frequent :—

Equisetum arvense. Salix lanata. S. herbacea. S. phylicifolia. Silene acaulis. Potentilla crantzii. Vaccinium uliginosum. Empetrum sp. *Bartsia alpina. Euphrasia* sp. *Erigeron uniflorus. Taraxacum* sp.

occasional :—

Poa pratensis agg. *Poa alpina* var. *vivipara. Festuca rubra. Carex nigra. Luzula spicata. Cerastium alpinum. Ranunculus acris. Cardamine pratensis. Sedum rosea*, leaves only. *Saxifraga hirculus. Pyrola minor. Cassiope hypnoides. Armeria maritima. Pedicularis flammea. Veronica alpina* var. *australis. Galium pumilum.*

rare :—

Phleum alpinum. Deschampsia flexuosa. Rumex acetosa. Gentianella tenella.

Mosses collected from this habitat in addition to *Drepanocladus uncinatus* were *Sphagnum teres, Polytrichum juniperinum, P. commune, Tortula ruralis, Desmatodon latifolius, Pohlia cruda, P. drummondii, Bartramia ithyphylla* and *Brachythecium reflexum.*

(b) In a wet boggy place below the nest-mound.

abundant :—

Drepanocladus aduncus, in water. *Calamagrostis stricta. Eriophorum scheuchzeri. Carex rariflora. C. nigra.*

frequent :—

Potentilla palustris.

(3) *A typical tundra-mound in the middle of a bog with adjoining shallow tarns.*

(a) The mound, well drained and fissured and eroded in places. *Empetrum* sp., almost dominant.

abundant :—
Rhacomitrium canescens. Salix glauca. S. herbacea. S. phylicifolia. Polygonum viviparum. Cassiope hypnoides.
frequent :—
Equisetum arvense. Festuca vivipara. Kobresia myosuroides. Carex bigelowii. Tofieldia pusilla. Salix lanata. Cerastium alpinum. Silene acaulis. Thalictrum alpinum. Vaccinium uliginosum. Armeria maritima. Bartsia alpina. Euphrasia sp. *Pedicularis flammea.*
occasional :—
Calamagrostis stricta. Deschampsia alpina. Poa alpina. P. alpina var. *vivipara. P. pratensis* agg. *Luzula spicata. Luzula* sp.

(b) Species found on the damp bare patches of erosion, or in the cracks or on bare flat patches near water.

abundant :—
Koenigia islandica.
frequent :—
Equisetum arvense. Minuartia stricta.
occasional :—
Juncus biglumis. Saxifraga cespitosa. S. hirculus. S. stellaris.
rare :—
Oxyria digyna.

(c) In the wet moss-covered area fringing a tarn.

dominant :—
Acrocladium giganteum, dominant on ground. *Carex rostrata*, dominant at its level.
abundant :—
Calamagrostis stricta. Carex rariflora.
frequent :—
Mnium cinclidioides. Acrcdladium stramineum. Eriophorum scheuchzeri. E. angustifolium. Carex nigra. Salix phylicifolia.
occasional :—
Polygonum viviparum. Cardamine pratensis.

(d) In the shallow water at edge of tarn.

dominant :—
Carex rostrata.
abundant :—
Eriophorum angustifolium.

(4) *Sunny slope leading from heath above to a stream below.* This is the typical heath bank.

abundant :—
Salix herbacea. Koenigia islandica, on bare patches. *Polygonum viviparum. Cassiope hypnoides. Empetrum* sp.
frequent :—
Equisetum arvense. E. variagatum. Hierochloë odorata, leaves only. *Poa alpina. Festuca rubra. Carex bigelowii. Salix glauca. S. lanata. S. phylicifolia. Cerastium alpinum. Sagina procumbens. Silene acaulis. Ranunculus acris. Thalictrum alpinum. Epilobium anagallidifolium. Vaccinium uliginosum. Armeria maritima. Bartsia alpina. Euphrasia frigida* var. *pusilla.*

occasional :—

Botrychium lunaria. *Salaginella selaginoides*. *Phleum alpinum*. *Deschampsia alpina*, damp place at bottom of the slope. *Trisetum spicatum*. *Poa alpina* var. *vivipara*. *Carex rariflora*. *Juncus arcticus*, damp place at bottom of the slope. *J. biglumis*. *Luzula spicata*. *Tofieldia pusilla*. *Rumex acetosa*. *Cerastium cerastoides*, in wet mossy place at bottom of the slope. *Sedum rosea*, leaves only. *Saxifraga cespitosa*. *S. nivalis*. *S. stellaris*. *Sibbaldia procumbens*. *Potentilla crantzii*. *Geranium sylvaticum*. *Angelica archangelica*, leaves only. *Pyrola minor*. *Gentianella tenella*. *Gentiana nivalis*. *Pedicularis flammea*. *Veronica alpina* var. *australis*. *Erigeron uniflorus*. *Gnaphalium supinum*. *Taraxacum* sp.

rare :—

Deschampsia flexuosa. *Juncus triglumis*, on muddy patch at bottom of the slope. *Lychnis alpina*. *Hieracium alpinum*.

Mosses collected from this habitat were *Blindia acuta*, *Rhacomitrium canescens*, *Pohlia cruda*, *Mnium* sp., *Bartramia ithyphylla*.

Liverworts collected from this habitat were *Pleuroclada albescens* and *Scapania curta*.

(5) *Typical Empetrum-Salix tundra near Base Camp.*

abundant :—

Salix herbacea. *Polygonum viviparum*. *Cassiope hypnoides*. *Vaccinium uliginosum*, locally abundant. *Empetrum* sp.

frequent :—

Equisetum arvense. *Festuca rubra*. *Carex bigelowii*. *Salix glauca*. *S. lanata*. *Cerastium alpinum*. *Silene acaulis*. *Thalictrum alpinum*. *Armeria maritima*. *Bartsia alpina*.

occasional :—

Botrychium lunaria. *Selaginella selaginoides*. *Trisetum spicatum*. *Poa alpina* var. *vivipara*. *Kobresia myosuroides*. *Luzula spicata*. *Tofieldia pusilla*. *Koenigia islandica*. *Lychnis alpina*. *Dryas octopetala*. *Gentianella tenella*. *Euphrasia frigida* var. *pusilla*. *Pedicularis flammea*. *Pinguicula vulgaris*. *Galium pumilum*. *Taraxacum* sp.

rare :—

Betula nana. *Saxifraga hirculus*.

A moss collected from this habitat was *Rhacomitrium canescens*.

(6) *A sandy bank at the foot of a gravelly hill.*

abundant :—

Equisetum arvense. *Poa alpina* var. *vivipara*. *Festuca rubra* (including var. *mutica*). *Salix glauca*, locally abundant. *S. lanata*, locally abundant. *S. phylicifolia*, locally abundant. *Cerastium alpinum*. *Silene maritima*. *S. acaulis*. *Cardaminopsis petraea*. *Armeria maritima*.

frequent :—

Deschampsia alpina. *Rumex acetosa*. *Thymus drucei*. *Galium pumilum*.

occasional :—

Trisetum spicatum. *Poa glauca*. *P. alpina*. *Festuca vivipara*. *Luzula spicata*. *Polygonum viviparum*. *Arenaria norvegica*. *Lychnis alpina*. *Draba norvegica*.

rare :—

Carex maritima.

(7) *The gravelly hills*

Much time was spent on these hills in working with the geese, and several were therefore well studied. TABLE 1 gives relative frequencies of the plants on five of the hills. Occasionally there were bands of denser vegetation where the soil appeared to be more stable, and these are referred to as terraces (t) in the table.

The typical plants of this habitat, in order of decreasing abundance were :— *Silene acaulis. Festuca rubra. Thymus drucei. Salix herbacea. Saxifraga oppositifolia. Salix glauca. Cardaminopsis petraea. Galium pumilum. Silene maritima. Armeria maritima. Luzula spicata. Cerastium alpinum. Poa glauca. Rumex acetosa. Dryas octopetala. Agrostis stolonifera. Juncus trifidus.*

TABLE I.—The frequencies of species on the gravelly hills

Species	Locality				
	A	B	C	D	E
Botrychium lunaria	—	r(t)	—	—	—
Equisetum arvense	—	—	o	—	—
E. variegatum	o	—	—	—	—
Agrostis stolonifera	—	—	f	r	f
Deschampsia alpina	r	—	—	—	—
Poa glauca	o	—	f	o	f
P. alpina	—	—	—	r	—
P. alpina var. *vivipara*	o	—	o	—	—
Festuca rubra (including var. *mutica*)	a	f	a	f	a
F. vivipara	—	—	f	—	o
Kobresia myosuroides	—	—	—	—	o
Carex maritima	f	—	—	—	—
C. bigelowii	o	—	—	r	o
Juncus trifidus	—	r(t)	—	f	o
Luzula spicata	o	o	o	o	f
Salix glauca	a	—	a	f	o
S. lanata	—	—	o	—	—
S. herbacea	o	a	o(t)	a	a
S. phylicifolia	—	—	o	o	—
Rumex acetosa	f	—	f	—	o
Polygonum viviparum	—	—	—	—	o
Cerastium alpinum	o	—	o	f	f
Minuartia rubella	r	—	o	—	o
Arenaria norvegica	r	—	—	r	—
Lychnis alpina	—	—	o	—	o
Silene maritima	f	—	a	o	o
S. acaulis	a	a	a	a	a
Cardaminopsis petraea	f	o	f	f	o
Saxifraga cespitosa	—	—	r(t)	r	o
S. oppositifolia	o	f	o	a	f
Dryas octopetala	o(t)	o(t)	r(t)	—	f
Empetrum sp. (*E. hermafroditum* or *E. nigrum*)	—	—	—	—	o(t)
Armeria maritima	f	—	f	f	o
Thymus drucei	a	a	a	r	a
Galium pumilum	f	o	f	r	f
Taraxacum croceum	r	—	—	—	—
Rhacomitrium canescens	—	a	—	f	o

Localities : A = Arnarfellsalda ; B = Hjartarfellsalda ; C = Oddkelsalda ; D = near Södulfell ; E = near Bólstadur (1951 Base Camp).

Frequencies : a = abundant ; f = frequent ; o = occasional ; r = rare ; t = terraces (see text).

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Summary

The habitat of the largest known breeding colony of Pink-footed Geese (*Anser brachyrhynchus*) at Thjórsárver vid Hofsjökul is described. These botanical studies were made during the Wildfowl Trust's Second Expedition to Central Iceland during July and August, 1953. The distributions and frequencies of 155 species, sub-species, varieties and hybrids of vascular plants are given; and 37 of the most common mosses and 8 most common liverworts are listed. The plant communities with which the geese are most associated are analyzed. Several of the species have rarely been recorded before from Central Iceland, *Minuartia stricta* and *Littorella uniflora* being of special interest. A collection representing all the plants described has been deposited in the British Museum (Natural History), London.

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MARINE FUNGI : A REVIEW OF THE PRESENT POSITION*

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(Communicated by the Botanical Secretary).

(With 28 Text-figures)

The sea covers nearly three quarters of the earth's surface. This vast expanse has only been sampled here and there for marine fungi. Nevertheless, the results which have been obtained are beginning to form a picture, the outlines of which it is attempted to present here.

The term ' marine ' fungi will be interpreted in a broad sense. The seas are not of uniform salinity throughout, while some reference to the fungi of brackish and even fresh waters is essential to an understanding of the marine forms.

Like all other fungi, marine fungi depend on organic substrates for their growth. Their distribution is therefore dependent on the distribution of their plant or animal hosts or on the organic substances formed on their decay.

Some have been found in animal hosts, including sponges (Galtsoff, 1940), shrimps (Phaff, Mark & Williams, 1952), blue crabs (Couch, 1942), pea crabs (Atkins 1929, 1954, 1955) and their eggs, on oysters (Hunter, 1920 ; Hewatt & Andrews, 1954), in clams (Kobayashi, Tsubaki & Soneda, 1953), on clam and oyster larvae (Davies *et al*, 1954 ; Vishniac 1955 *b*), on the Oyster drill (Vishniac, 1958), on fish such as herring, flounder and mackerel (Sproston, 1944) and on copepods in the zooplankton on which fish feed (Apstein, 1911 ; Jepps, 1937 ; Vallin, 1951).

A larger number have been recorded as saprophytes, parasites or systemic endophytes of algae of all kinds, from diatoms and small filamentous forms to the larger seaweeds, while many attack plant products such as wood and rope in the sea (see works of Petersen, Sutherland, Sparrow, Barghoorn & Linder, Meyers, Johnson & Meyers for major lists and references).

In addition, some microscopic, free floating forms occur in the sea, perhaps not directly attached to any surface (Vishniac, 1956).

The marine muds the infra-littoral, littoral and supra-littoral sands and other soils subject to the influence of the sea such as salt marsh soil and sand dunes have been investigated (Elliott, 1930 ; Sparrow, 1937 ; Höhnk, 1952, 1954 *a* ; Höhnk & Aleem, 1953, Harder & Ubelmesser 1955 ; Chesters, Apinis & Turner, 1956 ; Grein & Meyers, 1958).

Even the air over the ocean has been sampled for fungus spores, but, as spores of fungi can be carried very long distances by the wind, the results are not decisive (Rittenberg, 1940 ; Zobell, 1942 ; Blunt, 1955). Re-reading Rittenberg's list in the light of subsequent work, it does appear to contain a high proportion of forms common in the sea as well as on land.

Geographically, only small, scattered areas on the coasts of W. Europe, Russia (Black Sea and Arctic Ocean), Japan, Australia, Tasmania, India N. America (Pacific and Atlantic seaboard) and Macquarie Island in the Antarctic have been investigated. In depth, samples have been taken in the ocean from the surface down to a depth of 3450 m., many miles from the nearest land.

Going back in time it has even been suggested that the curious cavities in the bones of fossilized marine reptiles from the Trias to the Tertiary and in fossilized fish scales were caused by a marine fungus (references in Höhnk 1958)

* Paper read to the Society in January 1959.

Many of the PHYCOMYCETES are aquatic fungi and it might therefore be expected that, if any fungi can live in the sea, this class would be represented. All the earlier records of this group are of parasites on seaweeds and marine animals. Such finds were occasional and sporadic. The earlier literature was summarized by Petersen (1905) who himself added 15 species from Denmark. The chances of detecting these microscopic fungi are increased by bringing suitable pieces of seaweed into the laboratory and keeping them under observation for some time in dishes of artificial sea-water. If any activity is noted, such as the emergence of zoospores, further appropriate techniques can be applied (Kobayashi & Ookubo, 1953). New marine fungi, mainly parasites, continue to be found by these methods of direct inspection, many of them by algologists and zoologists.

Sparrow has not only added directly to our knowledge of marine Phycomycetes (1934, 1936, 1937) by the addition of new species, but by a critical reappraisal of earlier records (1943). Not the least of his contributions lies in the application of new methods by which marine Phycomycetes may be isolated.

If suitable baits are placed in water, either in its natural habitat or in dishes in the laboratory, zoospores which had been liberated into the water by aquatic fungi attach themselves and grow on the substrate provided. By this method saprophytes and facultative parasites may be isolated.

The ' bait ' technique has been well exploited, for example, by Höhnk in a large scale, well organized investigation of the changes in the aquatic fungal population in two great transects, the first from the mouth of the R. Weser, Germany, to the open ocean and the second from re-claimed coast land to navigable coastal waters (1958, summarizing earlier reports). The brackish and sea-water fungi were then compared with those in the upper reaches of the river and its tributaries (1956 *a*), one of the aims of the investigation being to find out if the brackish water forms are transitional. Harder & Ubelmesser (1955) have baited out Phycomycetes from ground samples taken from transects starting from submerged habitats, across the tidal zone and dry strand to land settled with higher plants, in nine localities in the North Sea, Baltic and Mediterranean. The baits used in these investigations by Höhnk and by Harder & Ubelmesser included hempseed, linseed, rice, straw, wood, cellophane, hair, cray fish, crab shells, fish scales, flies, pollen of different Pinus spp. and Fern spores. This sounds a strange mixture, but in reality the items are well chosen to secure the growth of a wide variety of Phycomycetous fungi.

A third method is to plate out samples of sea-water or pieces of seaweed, or other substrate being examined, on a solid agar medium (Sparrow, 1937), but a disadvantage of this method is the contamination with marine bacteria. Over 90 per cent of the marine bacteria are gram negative (Zobell, 1946 ; Huddleston, 1955) and, by the suitable combination of penicillin and streptomycin, they can be entirely suppressed. Vishniac (1955 *b*, 1956), using a solid agar medium, spread just before use with these two antibiotics, has isolated members of the Myxomycetes, Phycomycetes, yeasts and moulds.

All of these methods are highly selective, but they have greatly increased our knowledge of marine Phycomycetes in recent years, especially those from America, Germany, France and Japan. There have been a few interesting papers from Britain but no large-scale, organized investigation, and even the suggestion of Sparrow in 1936, that the fluctuations in the phytoplankton (where not due to hydrographic factors) might be due to marine fungi, has not been fully investigated.

Isolation of marine Phycomycetes on baits or on solid, agar media gives an opportunity for experimental studies which mycologists are beginning to use and which physiologists and ecologists could now usefully exploit also.

Among the UNIFLAGELLATE PHYCOMYCETES the order CHYTRIDIALES is well represented in the sea. Its members are characterized by the possession of a very simple thallus consisting, in the majority, merely of the enlarged body of the infecting zoospore as in *Olpidium maritimum* isolated by Höhnk & Aleem (1953) on Pine pollen baits from saline, supra-littoral soil (Fig. 1). Sometimes a fine rhizoidal system is more or less well developed in addition as in *Chytridium polysiphoniae* (Fig. 2), commonly found on several red algae and one brown alga (Petersen, 1905; Sparrow, 1936; J. & G. Feldmann, 1955; Johnson, 1957). In these only one reproductive structure is formed, after which the whole body usually disintegrates. In a few chytrids, however, several centres of thallus organization are formed, some or all of which may ultimately be converted into reproductive organs as in *Nowakowskiella elegans* (Fig. 3) found in marine soils (Harder & Ubelmesser, 1955) as well as in decaying leaves (Sparrow, 1943). Asexual reproduction is always by posteriorly uniflagellate zoospores formed in zoosporangia which dehisce in various ways. Resting spores (or sporangia) are also known (Sparrow, 1943).

Of the 24 saprophytic chytrids isolated from nine localities on the North Sea, Baltic Sea and the Mediterranean by Harder & Ubelmasser (1955), more than half were common to all three seas. Gaertner (1954) found similar forms in saline soils from Africa, Sweden and central Europe. Of the species parasitic on seaweeds, some are common to the W. European coasts and the eastern coast of the U.S.A. (Petersen, 1905; Sparrow, 1934, 1936; J. & G. Feldman, 1955; Johnson, 1957 *b*), but the majority recorded by Kobayashi and Ookubo (1953, 1954) on the Japanese coast are described as either new species or new morphological forms, but one of these has subsequently been found on the American east coast (Johnson, 1957 *b*).

Comparing the species in different ecological habitats from ground submerged under the sea, across the sands and up to land settled with higher plants, Harder & Ubelmesser (1955) found that fewer species occurred in the submerged ground, but that there was no essential difference in the species of saprophytic lower Phycomycetes in the sea and sea strand on the one hand and in the land and freshwater on the other hand, or, for that matter, from the general chytrid ground flora from the equator to the polar circle.

Experimental work in which baits bearing chytrids isolated from saline soils were placed in freshwater as well as in sea-water showed that all could grow in both, but all developed better in freshwater except *Rhizophidium halophilum* (Ubelmesser, 1956) which developed as well in sea-water as in freshwater and attacked the baits more frequently in sea-water. *Rh. carpophilum*, the most common species found, attacked the baits equally well in fresh and salt water (Harder & Ubelmesser, 1955). Gaertner (1954) grew two isolates of *Phlyctochytrium* from saline soil in Africa in freshwater and in a range of different concentrations of sea-water. Both grew in sea-water with a salt content of more than 6 per cent, but optimum sporulation occurred at 3·2 per cent. Höhnk & Aleem (1953) found that *Olpidium maritimum* from saline soil could grow at all salinities from 0 ‰ to 28 ‰, but sporulation was most prolific between 7‰ and 13 ‰. (Salinity is defined as grams of total solids per kilogram of sea-water. Surface water of the open sea, away from the influence of inflowing freshwater, has a salinity of 33–37 ‰ (Zobell, 1946).)

Thus, the geographical, ecological and experimental evidence available combine to suggest that the Chytridiales can tolerate a wide range of salinity. Although more numerous in land and freshwater they are well established in the sea. Only the parasitic species and perhaps a few saprophytic species are distinct from terrestrial and freshwater forms.

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The order ANISOCHYTRIDIALES was founded by Karling (1943) for Phycomycetes possessing zoospores with a single anterior flagellum. (This order is referred to as the Hyphochytriales by some later authors.) *Anisolpidium ectocarpii* has an olpidioid, monocentric, holocarpic thallus inside the filaments of the brown alga *Ectocarpus*. It reproduces asexually by the liberation of anteriorly uniflagellate zoospores through an exit canal (Karling, 1943) and sexually by the union of endobiotic isoaplanogametes (Johnson, 1957 *c*). The The salinity of the water in which the fungus and its host occurred was recorded by Johnson as 22·9 ‰. *A. sphacellarum* (Kny) Karling and *A. rosenvingii* (Petersen) Karling are also parasitic on Phaeophyceae, but most of the other members of the order are on freshwater hosts or in soil.

Among the BIFLAGELLATE PHYCOMYCETES, the small order LAGENIDIALES has some representatives in the sea as well as in freshwater. The genus *Olpidiopsis* has some marine species (Sparrow, 1943), *Petersenia* is mainly marine (Petersen, 1905; Sparrow, 1934, 1936, 1943), while *Sirolpidium bryopsidis* and *Pontisma lagenidioides* are widespread marine species (Petersen, 1905; Sparrow, 1934, 1936, 1943; Kobayashi & Ookubo, 1953; J. & G. Feldmann, 1955; Johnson, 1957). They are mainly parasites.

In this order, the enlarged body of the infecting zoospore forms a thallus which may remain unicellular as in *Petersenia* (Fig. 5), or become segmented, each segment being usually transformed into a reproductive organ as in *Pontisma* and *Sirolpidium* (Fig. 4). Asexual reproduction by means of biflagellate zoospores liberated through emission tubes from the endobiotic zoosporangia occurs in all the marine species, but sexual reproduction has not been described with certainty in any of them, although it possibly occurs in *Petersenia pollagaster* and *Sirolpidium bryopsidis* (Sparrow, 1943).

Karling (1942) included the genus *Pontisma* in *Sirolpidium* and this is supported by the observations of Vishniac (1955 *a*).

Vishniac (1955 *b*) considers that *Sirolpidium zoophthorum* (Davis *et al.*, 1954) is obligately marine (or more probably, estuarine) and is 'not exactly stenohaline'.

The SAPROLEGNIALES is one of the important orders of freshwater fungi and one might expect to find it represented in the sea.

In this order the zoospores are biflagellate and often dimorphic. The primary zoospore is pyriform with two apical flagella and, after encystment, emerges as a secondary zoospore with two laterally attached flagella. There are various degrees of suppression of the first motile phase, or, in a few cases, the flagella may be lacking. These differences are among the criteria which are used to separate genera, while the division into families is based on thallus characters.

FIGS. 1–11.—Fig. 1. *Olpidium maritimum* Höhnk & Aleem. Zoosporangium and uniflagellate zoospores in Pinus pollen grains; after Höhnk & Aleem, 1953. Fig. 2. *Chytridium polysiphoniae* Cohn. Empty, operculate zoosporangium; after Johnson, 1957 *b*. Fig. 3. *Nowakowskiella elegans* (Nowak.) Schroeter. Portion of extramatrical part of polycentric plant; after Sparrow, 1933. Fig. 4. *Sirolpidium bryopsidis* (de Bruyne) Petersen. Thallus and zoosporangia; after Johnson, 1957 *b*. Fig. 5. *Petersenia lobata* (Petersen) Sparrow. Discharged sporangial thallus; after Johnson, 1957 *b*. Figs. 6, 7. *Thraustochytrium proliferum* Sparrow. Fig. 6. Liberation of non-motile spores. Fig. 7. Spores in biflagellate condition; both after Johnson, 1957 *a*. Fig. 8. *Atkinsiella dubia* (Atkins) Vishniac. Zoosporangia, empty except for a few encysted spores, within abdomen of a zoea; after Atkins, 1954 *b*. Figs. 9. 10. *Leptolegnia marina* Atkins. Fig. 9. Discharged zoosporangium with new one proliferating inside, some spores on gill leaflet; after Atkins, 1929. Fig. 10. Oogonium with one oospore and hypogynous antheridium; after Atkins, 1954 *a*. Fig. 11. *Pythium thalassium* Atkins. Hyphae, emission tubes bearing vesicles with zoospores and emission tubes after discharge of zoospores projecting from ovum of Pea-crab; after Atkins, 1955.

The families *Ectrogellaceae* and *Thraustochytriaceae* (Sparrow, 1943) are of particular interest since they contain mainly marine forms and combine a primitive, Chytrid-like thallus with a Saprolegniaceous type of reproduction.

The Ectrogellaceae includes *Eurychasma Dicksonii*, one of the first marine fungi to be recorded from the British Isles (Wright, 1879), and repeatedly reported since (e.g. Sparrow, 1934 ; Aleem, 1950 ; Bishop,1950) as a parasite of *Ectocarpus* and other marine algae including *Striaria*. The zoospore infects a superficial, vegetative cell of the host and causes it to hypertrophy. The enlarged, endobiotic thallus becomes entirely transformed into a zoosporangium which bursts open the host cell and liberates zoospores through one or two short, broad discharge tubes. The biflagellate zoospores may emerge in the primary phase, or they may encyst within the zoosporangium leaving a net of cyst walls behind when they emerge as secondary zoospores (Sparrow, 1943). Several species of Ectrogella are marine. *Ectrogella eurychasmoides* is a new species recently described by J. & G. Feldmann (1955) in a marine diatom, *Licmophora Lyngbyei* which grows epiphytically on *Pylaiella littoralis*. Here again there is a simple thallus which is completely transformed into a zoosporangium. The zoospores have their first motile phase and encystment within the zoosporangium. A thick-walled, resting stage is also present.

The Thraustochytriaceae have a rhizoidal system within the host while the zoosporangium, formed from the enlarged body of the zoospore, remains outside. These features are illustrated by *Thraustochytrium proliferum* (Figs. 6, 7) (Sparrow, 1936, 1943 ; Johnson, 1957 *a* and *b*). In this species the spores are motionless when discharged, subsequently becoming motile with two lateral flagella. Proliferation of a new zoosporangium occurs within the old empty one. Resting spores have been found.

The recently formed family *Haliphthoraceae* (Vishniac, 1958) contains members with a filamentous thallus which is holocarpic, that is, it is ultimately wholly used up in the formation of reproductive organs. It includes the marine species *Haliphthoros milfordensis*, parasitic in eggs of *Urosalpinx* and *Pinnotheres* and is said to be ' obligately marine ' since it will only reproduce in sea-water or in a synthetic approximation to sea-water and is, at the same time, euryhaline as it will grow vegetatively in a wide range of inorganic salt solutions which differ greatly from sea water. *Atkinsiella dubia* (Atkins) Vishniac has been transferred to this family from the Saprolegniaceae by Vishniac (1958). It infects eggs of marine Crustacea and has an intra-matrical mycelium which is eventually wholly used up in zoospore formation. The zoosporangia (Fig. 8) may bulge out of the host tissues and can be renewed by proliferation. The zoospores have their first, short swimming phase within the zoosporangium and encyst within it, and later emerge as biflagellate, secondary zoospores through discharge tubes, leaving the empty cyst walls behind. Gemmae have been observed but sexual reproduction has not been seen in this, (or any other) member of this small family (Atkins, 1954).

The *Saprolegniaceae* have a well developed mycelium, without constrictions, and are eucarpic. Their asexual reproduction is by biflagellate zoospores, with varying degrees of suppression of the motile phases. The zoosporangia are renewed by proliferation in different ways. The sexual reproduction is oogamous. Gemmae are often formed. They are mainly freshwater and terrestrial forms.

R. A. Couch (1951), working under my direction, investigated the Saprolegniaceae in the R. Rheidol, Wales. He found that just above the tidal region about a dozen species of Saprolegniaceae were present, but the number decreased towards the river mouth and in the harbour only *Aphanomyces laevis* remained, and this developed on baits in *surface* water whose salinity did not exceed 4 ‰ and was therefore only slightly brackish. *Saprolegnia ferax* was one of the species in the tidal portion of the river. This species was subsequently invest-

igated by Höhnk (1952, 1953). Höhnk (1953) found, on growing it in water of varying salinity, that it grew best and had a full life cycle in freshwater. At a salinity of 3 ‰ it lost its power of sexual reproduction, at 7 ‰ its asexual reproduction, at 13 ‰ the power to form gemmae and at 25 ‰ only feeble vegetative mycelium existed. It is therefore primarily a freshwater form and is only able to withstand the lower range of salinities with impaired efficiency. This is also true for another saprophytic member of the family, *Aplanopsis terrestris* (Höhnk, 1953).

It appears that parasitic members of the Saprolegniaceae are more successful in the sea. *Leptolegnia baltica* (Vallin, 1951) was reported as the cause of an epidemic infection of a small plankton copepod, *Eurytemora hirundoides;* and this adversely affected the herring fisheries in the Northern Baltic. The water in this area, however, contained only 0·4–0·6 per cent salt. *Leptolegnia marina* (Atkins, 1929, 1954) is a destructive parasite of the pea-crab occurring in mussels in estuaries in southern England. When placed in tanks of sea-water the fungus continued to grow and reproduce. The mycelium is mainly intra-matrical. The zoosporangia are formed from unchanged hyphae and open to the surface by discharge tubes. The zoospores have their first motile phase within the zoosporangium. Proliferation of the zoosporangium may occur. The sexual reproduction is oogamous with one, thick walled oospore (Figs. 9, 10).

It must be remembered that in the Saprolegniaceae, whose sexual reproduction is controlled by hormones diffusing through the medium in which they grow (Raper, 1952), turbulence of the water, quite apart from considerations of salinity, would in itself be an obstacle to successful sexual reproduction in extramatrical forms.

Another order of the biflagellate Phycomycetes, the PERONOSPORALES includes one family, the *Pythiaceae*, which has aquatic members and a few of these are marine.

Höhnk (1953, 1958) in his investigation of saprophytic Pythiaceae in the lower part of the R. Weser and out to sea, found that at Bremerhaven seven sexual forms developed on the baits, but that further seaward the number decreased rapidly, the last species to form oospores being *Pythium marinum*, *P. maritimum* and *P. salinum*. Of these, *P. maritimum* was the best adapted to saline conditions. Although it was euryhaline, its growth and reproductive optima occurred in mesohaline (> 7 ‰ to ± 18 ‰) conditions and Höhnk regarded it as a permanent inhabitant of such brackish waters. Further out to sea, only vegetatively sporulating mycelia of saprophytic Pythiaceae were found. They tended to settle on nets, baskets and rope in the sea.

Höhnk considered that since certain species were regularly found in brackish and sea-water habitats and had their growth and reproductive optima in saline conditions and since some of them differed in minor taxonomic rank (species, varieties and perhaps physiological races) from freshwater and terrestial forms, they could not be regarded as merely temporary inhabitants of saline waters, but rather as permanent or even endemic forms. On the other hand, the relatively small numbers, the euryhaline condition and the reduced life cycles of the majority of Pythiaceae in higher salt concentrations might suggest that the sea was not the *original* home of the Pythiaceae. The brackish estuarine waters act like a sieve selecting those genotypes in the river population which can tolerate saline conditions. Those which have passed successive tests of increasing salinity and have migrated to the sea have evidently been established there for some considerable time.

Parasitic members of the Pythiaceae include an asexual species of Pythium found in a plankton organism, *Calanus finmarchicus* in some Norwegian fiords (Apstein, 1911). Atkins (1955) has described *Pythium thalassium*, parasitic and

saprophytic in the eggs of the pea-crab. The crabs were kept in tanks of sea-water whose salinity slightly exceeded the normal and was 36–37 ‰. The mycelium of the fungus was intra-matrical. Only asexual reproduction occurred, the zoosporangia being found inside the host and the zoospores differentiated in vesicles at the mouth of the exit tubes (Fig. 11).

Phycomycetes with non-flagellated spores (APLANATAE) including members of the MUCORALES have been isolated from marine or maritime soils (Elliott, 1930 ; Sparrow, 1937 ; Zobell, 1946 ; Ritchie, 1954 ; Harder & Ubelmesser, 1955). A detailed comparison of these with terrestial species needs to be made.

Ichthyosporidium hoferi, a member of the ENTOMOPHTHORALES is a parasite of many kinds of marine fish (Sproston, 1944) and possibly occurs on *Calanus finmarchicus*, a copepod, which may act as an intermediate host (Jepps, 1937). There is some evidence that the zygospores spread the infection outside the host, while the non-sexual spores of various kinds play their part within the host. Initial infection of fish is probably by way of the alimentary canal. There is an extensive literature on this parasite as it affects the herring industry of the U.S.A. (references in Johnson & Meyers, 1957).

The ECCRINALES are parasites in the alimentary canal of Arthropoda and have a coenocytic, usually unbranched, thallus and are attached to their host by a cup-like or disc-like holdfast. They form endogenous, non-flagellated spores. The order contains some parasites of marine animals (Wolf & Wolf, 1947 ; Dubosq, Léger & Tuzet, 1948).

The systematic position of the PLASMODIOPHORALES and LABYRINTHULALES is obscure. Sparrow (1943) places the former in the Phycomycetes, while Bessey (1950) includes both orders in the MYCETOZOA (MYXOMYCETES) which he considers to be more closely allied to the animal, than to the plant kingdom. Zoologists have classified them in the Protozoa, class Sarcodina (or Rhizopoda). A common characteristic of members of these orders is that they are naked during all stages of development except in the culminating spore stage (Bessey, 1950).

Many people will remember the dramatic disappearance of the eel-grass, *Zostera marina*, from the coasts of America and Europe during the nineteen-thirties. *Labyrinthula macrocystis* Cien was one of the two organisms often found associated with the dying eel-grass and was held to be responsible by Renn (1935, 1936) and Young (1938, 1943). The other organism was a Pyrenomycete, *Lulworthia halima* (Mounce & Diehl, 1943 ; Cribb & Cribb, 1955), and it was not invariably present. Whether either of these organisms was responsible, or whether adverse environmental factors, senescence, or some combination of these factors was the cause of the dying-out of the eel-grass has not been satisfactorily explained (Tutin, 1950).

Other species of *Labyrinthula* have been found in the sea (Jepps, 1931 ; Sparrow, 1936 ; Young, 1943 (with critical notes of earlier records) ; Vishniac, 1955, 1956 ; Chadefaud, 1956). Chadefaud distinguishes a freshwater genus *Labyrinthorhiza* from the marine genus *Labyrinthula* str. sensu, both formerly included in *Labyrinthula* Cien. In *Labyrinthula roscoffensis*, in *Ectocarpus*, and *Taonia*, the naked, spindle-shaped cells are enclosed in rigid, non-living tubes.

Labrinthula macrocystis on *Zostera marina* has a wide salinity tolerance (0–32 ‰ chlorinity) according to Young (1943), but Vishniac (1955), working with other species presumably, says that the Labyrinthulales are stenohaline, developing only in a rather narrow range of salinities.

Several species of *Plasmodiophora* and of *Tetramyxa* occur on marine Angiosperms (Ferdinansen & Winge, 1913, 1914 ; Setchell, 1924 ; Ostenfeld &

Petersen, 1930; Cook, 1932; J. Feldmann, 1940; Karling, 1942; Sparrow, 1943; G. Feldmann, 1958).

The systematic position of the ACTINOMYCETES is in doubt. Waksman & Henrici (1943) included three families, the *Mycobacteriaceae, Actinomycetaceae* and *Streptomycetaceae* in the order ACTINOMYCETALES which they placed in an intermediate position between Bacteria and Fungi Imperfecti. Chesters, Apinis & Turner (1956) have collected about 17 strains of laminarin and alginate decomposing Actinomycetes from decaying brown seaweeds, from masses of cast weed, from lagoon muds and from salt marsh soil and sand. Grein & Meyers (1958) examined completely submerged marine sediments and also wood and other substrates in the sea. The genera *Nocardia, Micromonspora* and *Streptomyces* were represented. Preliminary studies suggested that these were not autochthonous, but were terrestrial forms. About 50 per cent of the isolates exhibited some degree of antibiosis against selected gram positive and gram negative bacteria.

Some ASCOMYCETES and FUNGI IMPERFECTI (many of which may be imperfect states of Ascomycetes), are common in the sea. In their vegetative condition, the septate mycelium of these forms is more frequently found on baits in the sea than the aseptate mycelium of Phycomycetes (Harder & Ubelmesser, 1955), and septate mycelium is also more common on baits in the sea than in brackish water (Höhnk, 1956, 1957).

Sutherland (1916 *a*) discussed the first records of marine Fungi Imperfecti and himself described nine species, most of them new, growing saprophytically on seaweeds. They were *Cladosporium algarum, Diplodina laminariana, Fusidium maritimum, Monosporium maritimum, Sporotrichum maritimum, Cercospora salina, Macrosporium laminarianum, Alternaria maritimum, Epicoccum maritimum. Macrophoma gymnogongri* can be added to this list (J. & G. Feldmann, 1940 *b*; Cribb & Herbert, 1954).

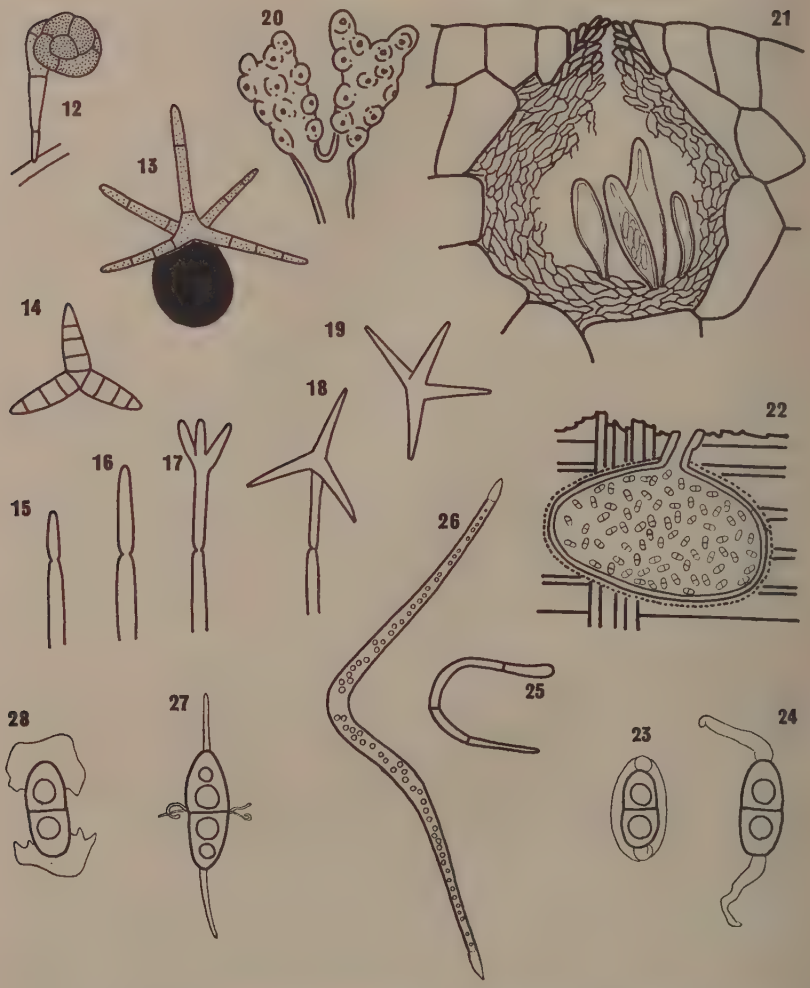
Fungi Imperfecti also occur on decaying salt marsh plants and in salt marsh soil (Elliott, 1930). Sparrow (1937) isolated species of *Penicillium, Aspergillus, Alternaria, Cephalosporium, Trichoderma, Cladosporium* (and also *Rhizopus* and *Chaetomium*) from marine muds, 18–220 m. below the surface of the sea, near Woods Hole, Mass., U.S.A., but as they were mainly well-known terrestrial species, he was doubtful whether they played an active part in the decomposition of organic materials present in the mud. Ritchie (1954) has pointed out that a terrestrial *Aspergillus* which grows in the sea is as much a marine fungus as a terrestrial fungus.

Barghoorn & Linder (1944) described seven species of Fungi Imperfecti on wood submerged in the sea. Four were new species of the genera *Diplodia, Helicoma* and *Speira* and three were assigned to the new genera *Botryophialophora, Phialophoroma* and *Orbimyces*. Reports of other species from wood have been made by Wilson (1951), Ritchie (1954), Höhnk (1955), Johnson (1956 *b*), Nilsson (1957) and Kohlmeyer (1958 *a*).

Some of the lignicolous species have conidia of curious form. The coiled conidia of *Helicoma* (Fig. 12) are also found in fresh water species, and the branched appendages of *Orbimyces* (Fig. 13) and the tri- and tetra-radiate conidia of the un-named forms in Figs. 14–19 recall the conidia of freshwater Hyphomycetes (Ingold, 1942).

The marine members of the Fungi Imperfecti can be classified in all four of the commonly recognized form orders SPHAEROPSIDALES, MELANCONIALES, MONILIALES and MYCELIA STERILIA.

Among the HEMI-ASCOMYCETES, which includes those Ascomycetes which lack a fruit body, the yeasts or SACCHAROMYCETALES are well represented in the sea and the ENDOMYCETALES have one or two marine members.



FIGS. 12–28.—Fig. 12. *Helicoma maritimum* Linder. Coiled conidium. Fig. 13. *Orbimyces spectabilis* Linder. Appendaged conidium; after Linder in Barghoorn and Linder, 1944. Fig. 14. Conidium of unidentified Hyphomycete 'Y' on wood in the sea. Figs. 15–19. Stages in development of conidium of unidentified Hyphomycete 'X' on wood and rope in the sea (*Heliscus* sp. ?). Figs. 20, 21. *Mycosphaerella Pelvetiae* Suth. Fig. 20. Fruit bodies visible as *small*, black dots on receptacles of *Pelvetia canaliculata*. Fig. 21. Section of fruit body containing asci. Figs. 22–24. *Ceriosporopsis halima* Linder. Fig. 22. Section of fruit body containing ascospores, in wood; after Wilson, 1954. Fig. 23. Ascospore with folded appendages and enclosed in mucilage. Fig. 24. Ascospore with extended appendages. Fig. 25. *Trailia Ascophylli* Suth. Whip-like ascospore. Fig. 26. *Lulworthia* sp. Ascospore with terminal appendages. Fig. 27. *Peritrichospora integra* Linder. Ascospore with appendages. Fig. 28. *Remispora maritima* Linder. Ascospore with appendages.

The methods used in the isolation of yeasts have much in common with those used in the isolation of bacteria, so it is not surprising that the first records of yeasts in the sea were made along with bacteria. Fischer (1894) showed that the total number of micro-organisms in the sea (bacteria, yeasts and moulds), found by plating out drops of sea water on a solid agar medium, was greatest nearest the land, but yeasts were present in all samples of sea-water tested. This and other early work on marine yeasts is summarized by Zobell (1946).

Yeasts are known to occur on marine animals. For example, Phaff, Mark & Williams (1952) isolated from the shrimp species of *Rhodotorula*, *Trichospora*, *Torulopsis*, *Pullularia*, *Candida* and *Hansenula*, while Kobayashi, Tsubaki and Soneda (1953) have isolated species of *Rhodotorula*, *Candida* and *Torulopsis* (and also *Sporotrichum roseum* and *Pullularia pullulans*) from the little neck clam in Japan and found that all of the yeast species could tolerate 10 per cent Na Cl, and three of them 15 per cent Na Cl, in malt agar.

Marine yeasts are also found associated with seaweeds. Nadson & Burgwitz (1931) isolated yeasts including 15 varieties of 'white Torula' and two 'red Torula' and yeast-like fungi from the surfaces of *Laminaria saccharina*, *Alaria esculenta*, *Fucus vesiculosus* and other seaweeds. They considered some species of 'Torula' and *Endomyces vernalis* to be autochthonous species. Blunt (1955) studied the decomposition of the giant kelp, *Durvillea antarctica*, by micro-organisms on Macquarie Island in the Antarctic. He found Penicillia, bacteria, Protozoa and yeasts. The yeasts attacked the stored carbohydrates within the tissues and the Protozoa fed on the bacterial slime on the surface. Yeasts have been isolated from the surfaces of algae and from sea water using the plating technique with antibiotics by Vishniac (1956).

From open waters, 2–6 miles from the Indian coast, Bhat and Kachwalla (1955) obtained 74 species of yeasts belonging to the genera *Saccharomyces*, *Debaryomyces*, *Candida*, *Torulopsis*, *Rhodotorula*, *Cryptococcus* and *Trichospora*. *Candida tropitale* was the most common. Kriss & Nowashiloff (1954) found yeasts in the Black Sea at all levels, from the surface down to a depth of 1750 m. In the Pacific Ocean, 140 miles from the nearest land, yeasts were present in greatest numbers near the surface and in deeper waters they were in layers like the plankton (Höhnk, 1958). Yeasts have been reported from the Arctic circle at depths from 10 m. down to 3450 m. Thus yeasts are widespread in the oceans and probably extend from pole to pole. Do they rely for their nutrition on the minute quantities of organic compounds known to be dissolved in sea water or are they always associated with the surfaces of plankton organisms or minute particles of organic débris? Can they exist in oxygen poor layers of the ocean?

Among the Eu-Ascomycetes, characterized by the possession of a fruit body containing asci, there are few records of either the Plectomycetes or the Discomycetes in the sea. An unidentified Plectomycete was found on submerged wood by Johnson (1956) and some of the Aspergilli have a perfect stage, *Eurotium*, which can be classified here. The inoperculate Discomycete, *Orbilia marina* has been reported by Boyd (1901) on decaying *Ascophyllum nodosum* (Smith, 1908).

The major group of Eu-Ascomycetes found in the sea is the Pyrenomycetes. In these the asci are contained in fruit bodies with a small ostiole through which the ascospores are eventually shed. Other spore forms may occur in the life cycle.

The earliest records are of parasites, saprophytes and endophytes of seaweeds. The most important single contributor to our knowledge of these forms is undoubtedly Sutherland, who, in a series of papers (1914, 1915 *a* and *b*, 1916 *a* and *b*), summarized the previous records and described 17 species, many of them new, and three new genera, *Orcadia*, *Trailia* and *Lulworthia*. In Table 1, the marine Pyrenomycetes on some of the common, larger, brown seaweeds of

the British coast are listed in order to give some idea of the taxonomic and ecological range of these forms. Of the hosts, *Pelvetia canaliculata* is reached only by the highest spring tides, *Ascophyllum nodosum* and *Fucus vesiculosus* grow between high and low tide marks and the *Laminaria* spp. occur just below low water mark or in deep pools near low water mark.

TABLE I.—Marine Pyrenomycetes on some littoral Phaeophyceae on British coasts

Marine Pyrenomycete	Phaeophyceae	Authority
Mycosphaerella Ascophylli Suth.	*Pelvetia canaliculata* Dcne. & Thur.	Sutherland, 1915 *a*
Stigmatea Pelvetiae Suth.	,,	,, ,,
Pharcidia Pelvetiae Suth.	,,	,, ,,
Pleospora Pelvetiae Suth.	,,	,, ,,
Orcadia pelvetiana Suth.	,,	,, 1915 *b*
Didymosphaeria pelvetiana Suth.	,,	,, ,,
Dothidella Pelvetiae Suth.	,,	,, 1914
Mycosphaerella Ascophylli Cotton	*Asophyllum nodosum* Le. Jol.	Church, 1893 ; Cotton, 1908
Orcadia Ascophylli Suth.	,,	Sutherland, 1914
Trailia Ascophylli Suth.	,,	,, ,,
Didymosphaeria fuciola Suth.	*Fucus vesiculosus* Linn.	,, 1915 *b*
Orcadia sp.	,,	,, 1916 *b*
Lulworthia fuciola Suth.	,,	,, ,,
Lulworthia salina (Linder) Cribb & Cribb	,,	Wilson, 1951
Hypoderma Laminariae Suth.	*Laminaria saccharina* Lamour	Sutherland, 1914
Ophiobolus Laminariae Suth.	*Laminaria digitata* Lamour	,, ,,
Pleospora laminariana Suth.	*Laminaria* sp.	,, 1916 *b*
Rosellinia laminariana Suth.	,,	,, ,,

Marine Pyrenomycetes occur on other Phaeophyceae and on Chlorophyceae and Rhodophyceae. They are found on marine Angiosperms such as *Zostera marina* and on salt marsh plants. Records on marine animals are rare, but Picard (1908, 1913) has recorded *Laboulbenia marina* on marine Carabidae.

Barghoorn and Linder (1944) described a very distinctive fungus flora on wood blocks submerged under the sea as bait for varying periods. Their finds included 14 new species and seven new genera, *Samarosporella, Ceriosporopsis, Remispora, Lentecospora, Halosphaeria, Peritrichospora* and *Halophiobolus* (antedated by *Lulworthia* Sutherland (Cribb & Cribb, 1955)).

The taxonomy of marine Pyrenomycetes has been reviewed by Meyers (1957) and new specific limitations, based almost entirely on spore size, suggested. A useful literature list on marine fungi has been compiled by Johnson & Meyers (1957) in which recent work is cited. Although comparatively little work has been done on development (Wilson, 1954 ; Lloyd, 1958 ; Meyers, 1956) it is clear that the species described can be assigned to recognized orders such as the SPHAERIALES, HYPOCREALES, PSEUDOSPHAERIALES, DOTHIDEALES and LABOULBENIALES. The Ophiostomataceae may be included in Plectascales (G. Feldmann, 1957) or in the Sphaeriales.

In relation to their substrate the marine Pyrenomycetes include all gradations between saprophytism and parasitism, while a few are systemic endophytes of seaweeds. In the association between *Guignardia Ulvae* and *Ulva Californica* and between *G. Alaskana* and *Prasiola borealis*, the fruit bodies of the fungus develop all over the algal thallus (Reed, 1902). In the association between *Mycosphaerella Ascophylli* and *Ascophyllum nodosum* (Cotton, 1908) and between *M. Pelvetiae* and *Pelvetia canaliculata* (Sutherland, 1915) the mycelium

is constantly present and permeates the whole alga but the fruiting bodies of the fungus are formed only on the receptacles of the seaweed (Fig. 20) and the ascospores and the oospheres are discharged at about the same time. Comparisons have inevitably been drawn between these dual organisms and lichens and with the composite organism *Cladophora—Blodgettia* (Sutherland, 1915; Smith & Ramsbottom, 1915; Feldmann, 1938; Mattick, 1953).

The fruit bodies of marine Pyrenomycetes are, for the most part, sunken within the substrate, opening to the surface only by a small ostiole. In terrestrial species asci usually pass up to the opening, one at a time, and squirt out the ascospores which may then be carried further by air currents. The question arises whether asci can actively discharge their spores under the sea. They have been shown to do so in *Leptosphaeria discors* (Johnson, 1956 *a*) although the method in this case differs in some respects from that usual for bitunicate asci. In *Ceriosporopsis* (Fig. 22) and some other genera the ascus walls deliquesce and liberate the ascospores into the inside of the fruit body and from there they ooze out of the ostiole (Barghoorn & Linder, 1944; Wilson, 1954). The main biological requirement is that there should be some mechanism to bring the reproductive units out on to the surface of the substrate so that they can be washed away by the sea and dispersed.

The ascospores of some marine Pyrenomycetes are well adapted by their form and by the presence of oil drops as food reserves for floating in the sea, their form also enables them to become entangled in objects which they may encounter, while the presence of mucilage sheaths or mucilaginous appendages may facilitate attachment (Figs. 23–28). The ascospores of many marine Pyrenomycetes germinate within a short time after discharge.

The physiology of some lignicolous marine fungi was investigated by Barghoorn (1944). In the 14 species of Pyrenomycetes and Fungi Imperfecti tested, the preferred Carbon sources were cellulose, pectin and starch, but a variety of sugars could also be utilized. The temperature optima for growth of the mycelium were high, only three of those investigated having optima below 25° C. The most outstanding fact, however, was that these fungi could all grow, not only on media made up with sea-water, but with sea-water concentrated to one third of its bulk.

More recently Ritchie (1957) has investigated the relationship between temperature and salinity and considers that a further extension of such studies might help to explain the distribution of marine fungi. Gustaffson & Fries (1956) studied the salinity, carbon, nitrogen, yeast and thiamine requirements of seven marine, lignicolous fungi. Most grew in both distilled water and sea-water and only *Halophiobolus opacus* Linder needed sea-water. Five required thiamine and asparagine was generally preferred as a nitrogen source to ammonium compounds or nitrates. Reynolds and Meyers (1957) state that several genera of lignicolous marine fungi grow well on a medium containing glucose, thiamine, biotin and asparagine (quantities not stated) and that wood flour or powdered cellulose can be substituted for glucose, often with an increase in reproductive capacity.

Further information on the salinity requirements of wood inhabiting marine fungi is furnished by Höhnk (1955) who measured the salinity of the waters in which they were found. Almost all were present in both brackish and sea-water.

In general, the marine Pyrenomycetes on wood can usually tolerate brackish water on the one hand and concentrated sea-water on the other hand, and under natural conditions, must often be obliged to do so.

In wood infected by species of *Ceriosporopsis* and *Lulworthia* there is a softening of the outer layers of the wood. The hyphae form bore holes through the walls of the wood elements and fine hyphae are also often seen in the middle, mainly cellulose layer of the secondary wall, often following the spiral course

of the cellulose fibrils (Barghoorn & Linder, 1944 ; Wilson, 1956, Kohlmeyer, 1958 *b*). This type of rot is known as ' soft rot ' (Savory, 1954). These observations have been made on naturally infected wood in the sea, where several species may be present simultaneously, so that the effects observed cannot yet be ascribed to particular species, but attempts at pure cultures are now being made.

Most marine fungi soften only the surface layers so that the wood is gradually eroded by the sea. *Lindra inflata*, however, attacks the medullary rays (Wilson, 1956). Becker & Kohlmeyer (1958) have described some Indian species, the commonest of which was *Halosphaeria quadricornuta* which rapidly destroyed the light, porous wood of fishing craft.

Attacks by the wood-boring crustacean, *Limnoria lignorum*, the gribble, frequently follow attacks by marine fungi and young gribble have been seen in the empty perithecial cavities of *Ceriosporopsis cambrensis* after they had enlarged the entrance through the neck (Wilson, 1954). The association between marine fungi and *Limnoria* has been elucidated by Becker, Kampf & Kohlmeyer (1957). Although fresh, fungus-free wood can be tunnelled, it alone is an insufficient source of food. In nature, fungal mycelium is invariably found in the wood round the tunnels and conidia of *Helicoma* have been found in the excrement of *Limnoria*, showing that this fungus had been eaten. Experiments show, first that the fungus is a source of food (although it alone, like wood alone, is insufficient), and secondly, that the mycelium of the fungus makes some fraction of the wood utilizable (presumably by decomposing part of the cellulose). So the gribble needs, for a balanced diet, both the wood and the marine fungi growing in it. This seems to be a case of ' ecto-symbiosis ' ; the gribble benefits in its nutrition and the fungus by the dispersal of its spores within a rich food supply. This association creates a new basis for the control of *Limnoria*.

Ritchie (1954), and Reynolds & Meyers (1957, 1958) have also made some contribution to our knowledge of the connection between marine fungi and wood borer attack.

It is well known that many LICHENS whose fungal component is an Ascomycete form an important element of certain maritime communities. In Britain these include grey, fixed dunes, rocks and cliffs exposed to sea and spray, and shingle beaches. In the last two the lower lichen zones, which include species of *Verrucaria*, are submerged at spring tides or at all tides ; the lichens of these lower zones can properly be regarded as marine.

Special mention must be made of the Antarctic Pyrenocarpous lichen *Verrucaria serpuloides* which, with an encrusting alga (Lithophyllum sp. ?), forms a sub-marine association below the lowest ebb tide (Lamb, 1948).

The BASIDIOMYCETES are virtually absent from the sea. Septate mycelium with clamp connections has been reported from salt marsh soil (Elliott, 1930) and a few Agarics occur on sand dunes (Ramsbottom, 1953 ; Höhnk, 1954 *b*). One of the Ustilaginaceae, *Melanotaenium ruppiae* has been reported on *Ruppia maritima* (G. Feldmann, 1959).

This survey shows that the main groups of fungi represented in the sea include members of the lower aquatic Phycomycetes and the Myxomycetes, the Ascomycetes (especially yeasts and Pyrenomycetes) and the Fungi Imperfecti. The marine fungi include only a few hundred species and form only a minute fraction of the total number of species in the fungi as a whole.

Did they originate in the sea which they now inhabit or are they terrestrial species which have secondarily adopted this habitat ? These are two separate issues.

The marine Pyrenomycetes and Fungi Imperfecti are, for the most part, representatives of well known terrestrial genera. The Pyrenomycetes can be

classed among the recognized orders and do not appear to show any particularly primitive characters. In my view they do not support the opinion, still held, that the Pyrenomycetes originated from Rhodophyceae. On the other hand there is no reason to suppose that they are very recent arrivals in the sea; they have been there long enough to evolve new species and even genera.

Similarly among the marine Phycomycetes, the Saprolegniaceae appear to be primarily freshwater forms, and the same applies, it seems to me, to the Pythiaceae, although these, with their greater tolerance of saline conditions have been rather more successful in establishing some members in the sea.

To the second question, whether fungi, like other living organisms, had their origin in the sea, it is necessary to turn to a consideration of the primitive Phycomycetes, especially the Uniflagellate chytrids and the simpler Biflagellates, and there are other simple forms of doubtful affinity such as the Labyrinthulales, the Eccrinales and the Actinomycetales. If any such groups had always lived in the sea one would expect them to be well represented in numbers, to be stenohaline and to have complete life cycles with full reproductive powers in the sea today. These criteria are not fully satisfied by any group although some of the Biflagellates come nearest to doing so, but relatively few collections of marine fungi have been made as yet, the methods of isolation favour the saprophytic forms and nearly all the work on salinity requirements has been carried out on saprophytes. No valid conclusions can be drawn from such biased results. More work is required on parasitic species.

The internal position of the mycelium within the substrate, efficient mechanisms for the liberation of the reproductive units to the surface and, in some Pyrenomycetes and Fungi Imperfecti, the wonderful forms of the spores with their floating, entangling and adhesive properties must have been important factors in the success of marine fungi. Physiologically, their ability to tolerate saline conditions seems to be the most important consideration. Ecologically they fulfil a role parallel to the marine bacteria.

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MICROMETEOROLOGY IN RELATION TO PLANT AND ANIMAL LIFE

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(Communicated by the Zoological Secretary).

Summary

Micrometeorology is the study of atmospheric processes at the earth's surface. If the leaves of plants and the skins of animals are regarded as extensions of that surface, micrometeorological principles can help the biologist to investigate the influence of physical environment on living material. Two examples are considered in illustration. First, the surface temperature of plants and animals and the cooling produced by evaporation are discussed in terms of heat-balance equations. Second, it is shown that the uptake of carbon dioxide by a field crop can be measured by a micrometeorological technique.

The Scope of Micrometeorology

At noon on the ninth of July 1958, the temperature recorded in a Stevenson screen at Rothamsted, 25 miles north of London, was 20° C. A few yards away, the air temperature immediately above a crop of sugar beet was a little higher—about 22° C.—while within the crop and a few inches above the soil surface it was as high as 25° C. Such large differences of temperature in the vertical are characteristic of crop microclimate. Maintaining screen height and moving horizontally instead of vertically, it would have been necessary to travel far that day to find a region with air temperatures consistently as high as those inside the crop: south to the shores of the Mediterranean; west to the coast of Florida.

This situation distinguishes micrometeorology from its parent study. The *macro*-meteorologist, whether physicist or forecaster, is concerned primarily with the large-scale redistribution of energy over the whole globe following unequal heating by the sun; and with the average pattern of climate which this redistribution produces. Horizontal temperature gradients are generally only a few degrees Centigrade in a thousand miles. The *micro*-meteorologist is concerned with the redistribution of energy at one particular point of the earth's surface. This redistribution takes place mainly in the vertical, and produces large temperature gradients close to the surface sometimes reaching several degrees Centigrade in a foot. Other meteorological elements such as vapour pressure frequently exhibit similar large gradients near the ground.

So there is nothing 'micro' about the *differences* in temperature and humidity and wind speed which micrometeorologists measure. The microscope is a window into a world of complex forms invisible to the naked eye: and in a comparable way the techniques of micrometeorology reveal a microstructure in the lower atmosphere undreamed of by instruments in the seclusion of a Stevenson screen. In illustration of one aspect only of this microstructure, Fig. 1 shows temperature profiles in a crop of sugar beet.

At 03.00 G.M.T. the minimum temperature was at the surface of the crop, and because, by definition, heat always flows from high to low temperature whatever the transfer mechanism may be, we can infer fluxes of heat from soil to surface and from air to surface. Meteorologists refer to the mechanism

responsible for such atmospheric heat transfer as ' turbulence ', the mixing of air in motion. Now if there were no other heat exchange mechanism in the system, the heat converging at the crop surface from above and below should have rapidly warmed the air at that level. In fact, the air cooled from 12·5° C. to 12·4° C. between 03.00 and 06.00. This implies that heat was being dissipated at approximately the same rate as it was being supplied by turbulence. The mechanism of this heat loss was the exchange of long-wave radiation between the leaves and the atmosphere. This is what is sometimes known as ' nocturnal cooling '—misleadingly, because it continues to be a

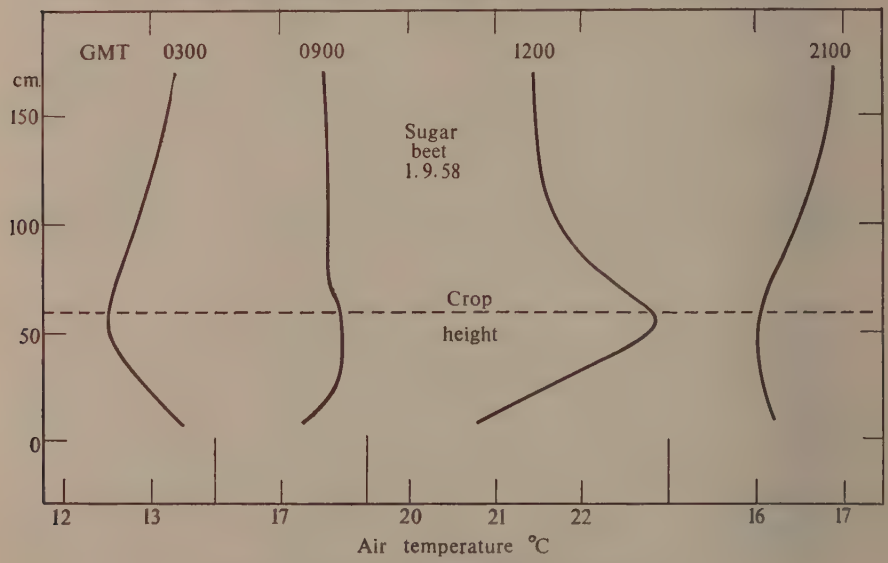

Fig. 1.—Variation of air temperature with height in a mature stand of sugar beet.

cooling process both day and night and is negligible only when the sky is heavily overcast. The process has been compared to a constant exchange of Christmas cards. The rate of exchange varies with temperature and cloudiness but the leaf always sends out more cards than it gets back.

Temperature gradients were reversed at noon when the crop canopy was absorbing heat in the form of short-wave radiation from the sun and re-distributing it by turbulence both to the soil and to the air. Absorbed short-wave radiation exceeds the long-wave radiative loss during most daylight hours in summer so that there is a net gain of radiant energy.

In one very important development of micrometeorology, the complexities of heat and vapour exchange within a crop are ignored : the crop is treated as a uniform flat surface and fluxes of heat, water vapour, and momentum between this surface and the air flowing over it are calculated from measurements of temperature, humidity and wind speed *above* the crop. This provides valuable information about mean effects but throws little light on the thermal relationship between an individual leaf and its environment. Both leaves and animals may be regarded as extensions of the earth's surface subject to the same physical laws of heat transfer as inert material. So any fundamental study of the interaction between life and microclimate is necessarily a micrometeorological enquiry into the redistribution of energy at one particular point of the

earth's surface. In a paper to the Linnean Society it seems appropriate to attempt a classification of living things according to the way in which they adjust themselves thermally to their environment, but this can be achieved only by using the simple language of physics to describe complicated biological processes which no physicist can ever fully understand.

The Heat Balance Equation

The starting point is an enumeration of all the heat transfer processes which operate when a body is in thermal equilibrium with its environment. First

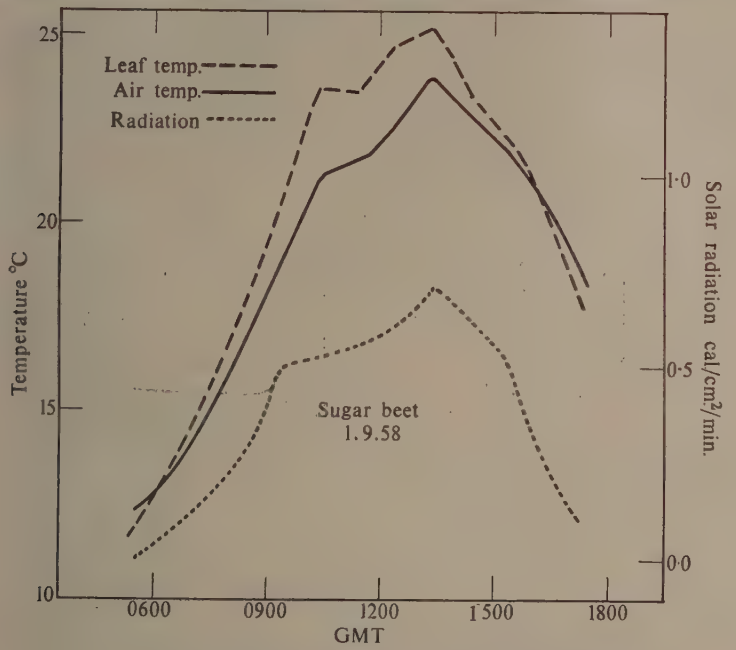

Fig. 2.—Diurnal variation of solar (short-wave) radiation, and of air and leaf temperature near the top of a sugar beet crop.

it receives short-wave radiation S from sun and sky in the wave-length range 0·3–3 microns of which only the 0·4–0·7 micron range is visible light, and a fraction α of this radiation is reflected from the surface. There is little variation in α for the green foliage of most species growing in temperate climates; reflectivity lies between about 22 and 27 per cent. Some desert species have a significantly higher reflectivity which may represent an adaptation to conditions of great heat stress. *Eurotia lanata* achieves a reflectivity of 40 per cent by a dense mass of white hairs; *Prunus andersonii* with reflectivity about 35 per cent does not look particularly white but has enhanced reflection in the infra-red beyond 0·7 microns (Monteith, 1959). The range for animals is much wider. Reflectivity is about 15 per cent for black Angus cattle, and 40 per cent for a (clean) sheep (Macfarlane, 1958), and pale human skin reflects about 50 per cent (Brunt, 1943). Corresponding data for insects are hard to find but figures for the visible part of the short-wave spectrum given by Rücker (1933) range from 5 per cent to 74 per cent for a white beetle (*Compsus niveus*), with an average of 22 per cent.

Leaves also transmit light ; 30 per cent transmission is an average figure for agricultural crops so transmission plays a very important part in the heat economy. Writing transmission β the net short-wave radiation received by a leaf or animal per unit area is $(1 - \alpha - \beta)\ S$. If S is measured on a horizontal surface—the standard meteorological procedure—an approximation is necessary to obtain the radiation received by a plant or animal.

The long-wave heat loss L, which takes place entirely in the infra-red part of the spectrum from 3 to 30 microns, can be calculated from surface tempera-

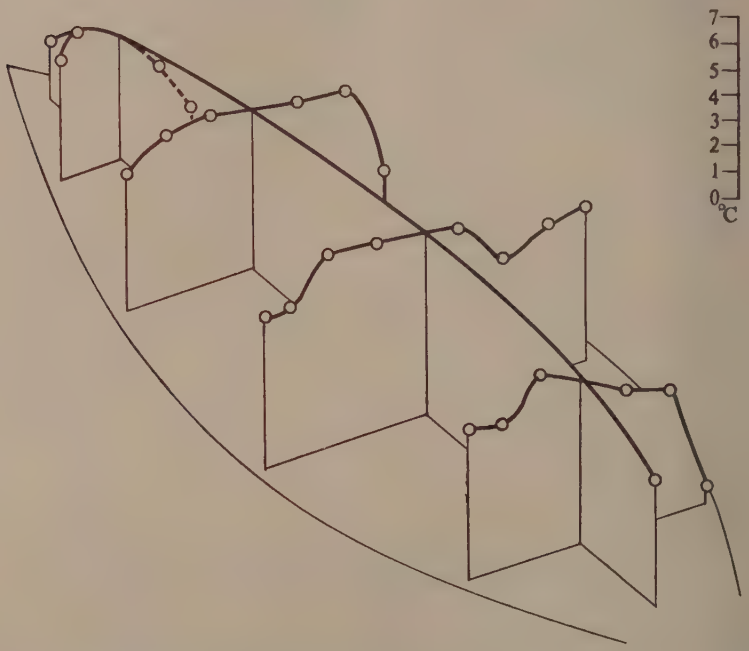

FIG. 3.—Temperature distribution (represented by height of vertical ordinate) for a leaf of *Canna indica*. Mean excess temperature 5·5° C. ; wind speed 3·3 m./sec. ; net radiation 0·97 cal./cm.²/min. (After Raschke, 1956.)

ture, because most natural objects have sufficiently rough surfaces to behave as black bodies radiating as the fourth power of absolute temperature. Similar calculations give the radiation received by an animal or leaf from a warmer soil surface and there are empirical formulae for estimating the long-wave flux from the atmosphere from surface data.

A hot body surrounded by colder air is cooled by convective heat transfer to the air from the body surface. Engineers relate this convective heat loss per unit area C to temperature difference T (surface) $-T$ (air) by a transfer coefficient h which is a function of wind speed and of the shape and size of the body such that $C = h \times (T_s - T_a)$. In the engineering literature there are empirical formulae giving h for cylinders, spheres, plates etc. which are extremely useful in estimating the heat balance of animals and leaves. But for a reason

which will appear shortly it is more convenient here to write $h = K/\lambda$ where K is a diffusion coefficient, regarding λ (which has the dimensions of length) as the effective thickness of the aerodynamic boundary layer—the thin skin of air surrounding a body which impedes the exchange of heat between the surface and the ambient air. The larger the body, the larger λ becomes and the greater must be the temperature difference to dissipate the same amount of heat.

The form $h = K/\lambda$ makes it possible to use a similar expression for the heat transfer by evaporation E. When a living organism transpires there is an internal resistance to the diffusion of vapour in addition to the resistance of the aerodynamic boundary layer. For a leaf, there is the resistance of stomata and of sub-stomatal cavities ; for an animal there is the analogous resistance of the tracheal system ; and for both animals and plants there is the resistance to the diffusion of water vapour through the cuticle. Ignoring biological complexity we can formally write the internal diffusion resistance of the organism as λ^* so that the transfer coefficient for water vapour becomes proportional to $K/(\lambda + \lambda^*)$. (The constant of proportionality is required simply to obtain consistent units.) For a leaf with negligible cuticular transpiration, λ^* is a function of stomatal diameter and number and as such has been successfully computed by plant physiologists. The same formalism does not appear to have been used in the study of animal transpiration where λ^* would be a function of such things as respiration rate, the behaviour of sweat glands, or the temperature dependent permeability of a waxy cuticle in insects.

With metabolism (M) and photosynthesis (P) the complete heat-balance equation becomes

$$(1 - \alpha - \beta)\, S + L + C + E + M + P = 0.$$

Written out in full in terms of temperature and vapour pressure differences this is a rather cumbersome equation. It can be considerably simplified by assuming that body temperature, that is the temperature of the transpiring surface, is equal to skin temperature. This may be a good approximation for a leaf and for animals whose body temperature is little different from that of the environment. But it may be unjustifiable for warm-blooded animals when a large body/air temperature difference is maintained by thermo-regulation. The heat balance equation then contains three terms, L, C, and E which are functions of surface temperature which can therefore be determined if all other variables are known. To recapitulate, the meteorological variables are

Short-wave radiation
Air temperature } from which atmospheric long-wave radiation can be
Vapour pressure } estimated
Wind speed
Temperature of ground

while the biological variables are

Reflectivity and transmissivity
Size
Shape
Internal diffusion resistance
Metabolism and photosynthesis

Having determined surface temperature it is possible to calculate the rate of evaporation and the amount of cooling which evaporation produces. Alternatively, if the evaporation rate is known, it would be possible to estimate

the internal diffusion resistance and hence to study changes in stomatal resistance, cuticular permeability, etc., in different environments.

The list of variables in the equation is formidable but to illustrate the type of practical calculation it permits, estimates have been made of the approximate heat balance of a small leaf, a cockroach (*Periplaneta americana*) and a Merino sheep, in one set of meteorological conditions corresponding to midday June sunshine in the British Isles, namely : solar radiation on horizontal surface 72 cal./cm.^{2}/hr, air temperature 25° C., ground temperature 30° C. relative humidity 50 per cent and wind speed 1·5 m./sec. For the leaf it has been assumed that the stomatal resistance is twice that of the boundary layer and transfer coefficients have been derived from the formula of de Vries & Venema (1954). For the insect and the sheep, values of transpiration and basal metabolism quoted in the literature have been used (Parry, 1951 ; Priestley, 1958) ; so the internal resistance need not be determined explicitly.

Table I shows the components of the heat balance in calories per square centimetre of surface per hour. Basal metabolism approaches a significant value only in the sheep : in cloudy weather it could dominate the sheep's heat balance. Metabolism of an insect in flight may be many times the basal value and may become a more important term than radiation even in bright sunshine (Rainey, Waloff & Burnett, 1957). There is a clear distinction between the way in which the energy of solar radiation is dissipated. The most effective mechanisms for heat loss are transpiration for the leaf, convection for the cockroach, and long-wave radiation for the sheep. The leaf behaves rather like a wet surface because the stomatal resistance is comparable with that of the boundary layer. The cockroach can conserve water and lose heat efficiently by convection because it is a small object with a high heat exchange coefficient. For the sheep, long-wave radiation is even more effective than convection and this implies a very high fleece temperature.

Plants and animals could therefore be classified by the way in which they lose heat in a hot environment : evaporators, convectors and radiators. In terms of existing nomenclature, evaporators and convectors will generally be ' poikilotherms ' with a variable body temperature similar to that of the air, whereas radiators will be ' homoiotherms ' with a high and more or less constant body temperature. Such a classification could never be hard and fast : plants change from evaporators to convectors when they wilt and the stomata close. And animals that behave in some conditions like convectors or radiators could conceivably become evaporators when covered in sweat.

Formally the distinction is

Evaporators	$\lambda^* \simeq \lambda$, λ small
Convectors	$\lambda^* \gg \lambda$, λ small
Radiators	$\lambda^* \geqslant \lambda$, λ large

Excess surface temperature can now be calculated from the heat balance data as shown in Table II which compares the excess temperature for a normal body with the excess that would be developed without transpiration. Comparison of the two figures gives transpirational cooling which is considerable for the leaf, slight for the sheep and negligible for the cockroach. The high surface temperature of the sheep occurs at the tips of the fleece and Australian workers have measured temperatures as high as 87° C. on a sheep's back (Macfarlane, 1958). Table II also shows the estimated surface temperature that would be obtained if the surface were covered with a film of water. This would reduce the temperature of both the leaf and the cockroach below that of the air, but the sheep would still be 3° C. hotter because for an animal of that size the heat transfer coefficient is small.

It has sometimes been stated in the biological literature that convection is proportional to surface area but this is not so. For cylinders the *total* convective heat loss is very nearly proportional to the square root of the diameter for constant temperature difference. It follows that the heat lost per *unit* area for unit temperature difference is seven times greater for the cockroach (diameter 1 cm.) than for the sheep (diameter 50 cm.). The only advantage of large animals is their very large heat capacity which enables a certain amount of heat to be stored in the body during the day and released at night. The camel, for example, can permit a rise in body temperature from 34° to 41° C. equivalent to heat storage of about 50 calories per square cm. of body area (Schmidt-Nielsen, 1958). This would be a very significant term in the heat balance, equivalent to the amount of solar energy received in the course of 1–2 hours of midday sunshine.

TABLE I

	+		−			
Calories cm^2/hr	Short-wave radiation	Metabolism	Long-wave radiation	Transpiration	Convection	Photosynthesis
Leaf	20	0·02	3	15	2	0·2
Cockroach .	32	0·2	6	0·4	26	..
Sheep	24	5	14	4	11	..

Short-wave radiation (horizontal), 72 cal./$cm.^2$/hr.
Air temperature, 25° C.
Relative humidity, 50 per cent.
Wind speed, 1·5 m./sec.

TABLE II

	T (surface) − T (air) ° C.			
	Normal	No transpiration	Wet surface	Cooling by transpiration
Leaf.....	+2	+11	−3	−9
Cockroach.....	+6	+6	−4	0
Sheep	+19	+22	+3	−3
Ideal wet-bulb...	−7	..	−7	−7

The data of Tables I and II are relevant to one set of meteorological conditions only, and within the scope of this paper it is impossible to consider the innumerable ways in which excess temperature and transpiration can vary with weather and with species. A few examples from an extensive literature must serve to illustrate the diversity of problems which can be discussed in terms of the heat-balance equation.

Leaf Temperature

Martin (1943) has demonstrated that when radiation is not a large term in the heat-balance of a leaf, transpirational cooling depends on wind speed and relative humidity, and leaf temperature may be as much as 12° C. below air temperature. At Rothamsted, small nickel resistance thermometers and thermocouples inserted in the midrib have been used to estimate the leaf temperature of agricultural crops. In bright sunshine leaves of potatoes and

sugar beet are generally several degrees warmer than the air, but in the late afternoon when transpiration still plays an important part in the heat balance with diminishing radiation, leaves often become colder than the air. Fig. 2 shows a typical set of measurements.

Working with a very large leaf of *Canna indica* (14 × 35 cm.) Raschke (1956) has shown that it is dangerous to generalize about leaf/air temperature differences from measurements made at one point of the surface. In bright

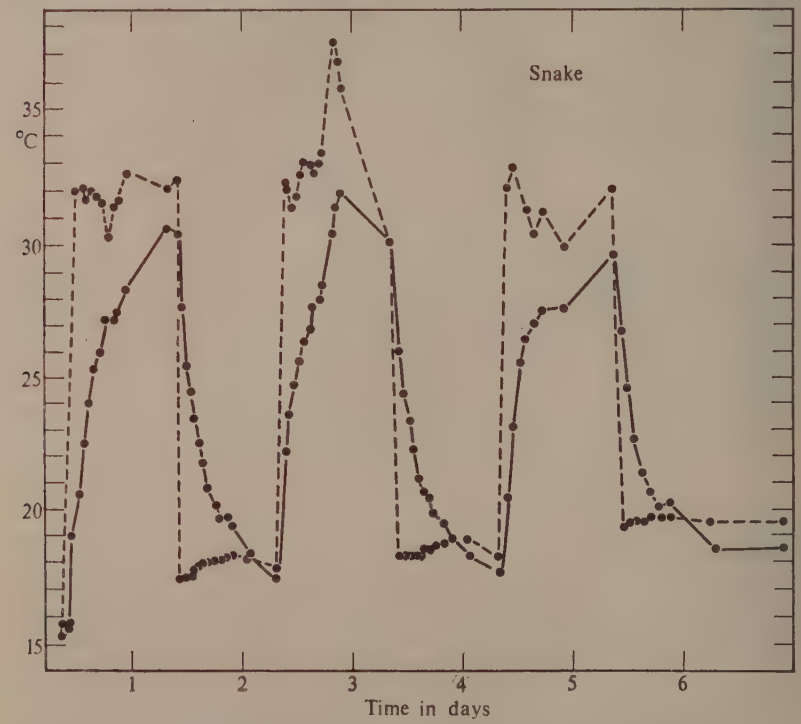

Fig. 4.—Rectal temperature of a snake (full line) and environmental temperature (dotted line). (After Benedict, 1932.)

sunshine the centre of the leaf was several degrees warmer than the periphery (Fig. 3) because heat exchange between leaf and air was most rapid round the edges. The ' heat transfer coefficient ' of the previous discussion is an average for the whole leaf concealing local variations in the coefficient and hence in temperature excess.

Animal Temperature

The practical difficulties of measuring representative leaf temperatures are surpassed in animal work by difficulties of quite a different kind. Commenting on Benedict's observations of the diurnal variation in body temperature of a snake, Gunn (1942) writes :—' the depression of body temperature of these large snakes in dry air is therefore clearly established, but it is nevertheless not possible to assign a representative set of values to the depression. In the first place it requires a number of men to handle a 5 m. python weighing 30 kg. when an attempt is to be made to take its oral and rectal temperatures.

Metabolic heat is increased because of the animal's struggles and heat is transmitted to the snake from the men's hands'!

Benedict (1932) found a diurnal variation in the rectal temperature of a snake from 17° to 31° C. when air temperature varied from 17° to 37° C. and this implies considerable storage of heat within the animal. During the day, body temperature was consistently below air temperature (Fig. 4), so Benedict assumed that transpiration was playing an important part in the heat balance, but this is contrary to other evidence and a simpler interpretation is possible.

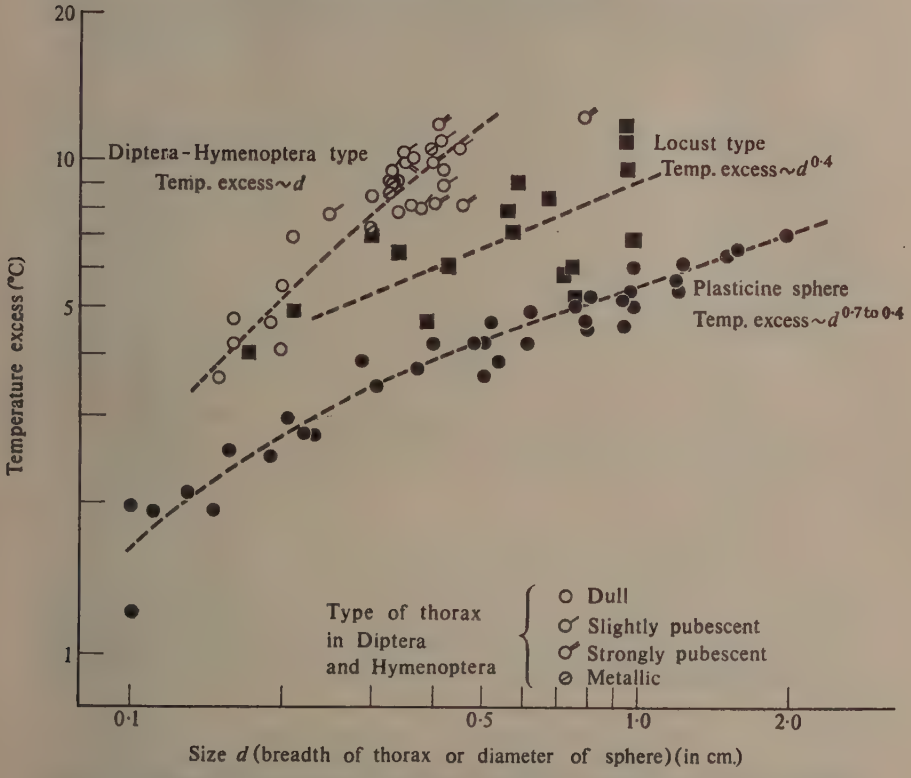

FIG. 5.—Variation in temperature excess with size for a series of insects and plasticine spheres on a log-log plot. Short-wave radiation 1·5 cal./cm.²/min.; wind speed 0·5 m./sec. (After Digby, 1955.)

At night the snake was warmer than the surrounding air because its internal heat capacity prevented it from cooling as rapidly. Conversely a time-lag in the heating of the snake's body each morning would give the observed temperature depression.

The relation of insect temperature to meteorological conditions has been thoroughly examined by Parry (1951) and by Digby (1955). Digby verified the theoretical prediction that excess temperature should increase with size by relating body temperature to thorax diameter (Fig. 5). Thorax temperatures were consistently higher than for plasticine spheres of the same diameter—an illustration of the difficulty of making the correct geometrical approximation when assessing heat exchange from a non-uniform body.

It has even been suggested that in body size and shape, Man shows climatic a aptation. The contrast between the squat body form of the Eskimo and the elongated form common in hot climates is particularly striking (Barnett, 1957).

Waterhouse (1955) in a study of the microclimate of grass drew attention to the dependence of insect temperature on wind speed in bright sunshine, inferring that in some situations it may be easier for an insect to keep cool by climbing into a windier climate near the top of a crop, than by seeking shade.

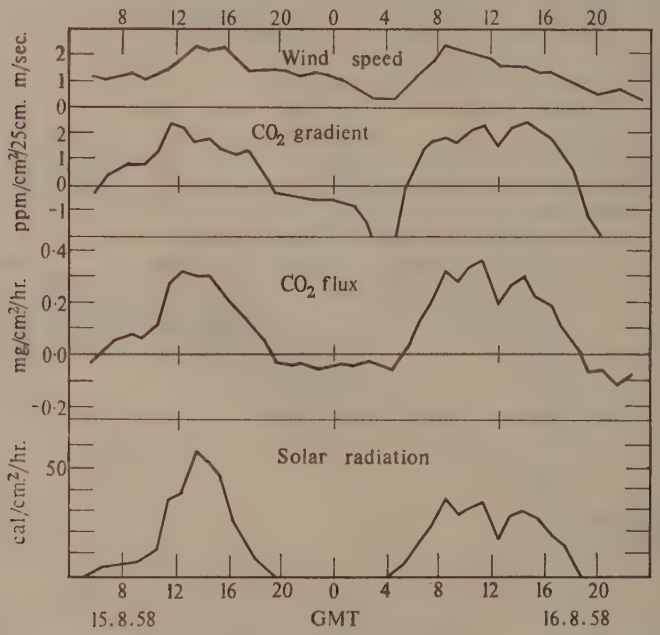

FIG. 6.—Variation of CO_2 flux and meteorological parameters over a crop of sugar beet for two August days. During the day CO_2 concentration in the air increases with height implying uptake by the crop. At night the concentration decreases with height as respiration supplies CO_2 to the atmosphere.

CARBON DIOXIDE UPTAKE BY FIELD CROPS

Another recently forged link between meteorology and biology is the study of crop growth in the field by a micrometeorological technique. This may appear a completely different problem from that of the thermal balance but it is formally very similar to it and the diffusive resistance of stomata and boundary layer are important parameters in the fundamental analysis. The rate of growth of a crop is generally measured as the dry matter increment in unit time and this can be related to the amount of carbon dioxide which the plant must assimilate from the atmosphere to build up the required carbohydrate. This carbon dioxide may come either from the ground or from the air. The measurement of the flux of water vapour in the air has been one of the main interest of micrometeorologists for the last ten years, and by a simple extension of the method they have recently been able to calculate CO_2 flux (Huber, 1952 ; Inoue, 1958). At Rothamsted in 1958 this flux was estimated over a sugar beet crop from the difference in CO_2 concentration between two levels above the crop (measured with an infra-red gas analyser) and from the wind

speed (measured with cup anemometers). Fig. 6 shows the variation of gradient and flux for two days in August and emphasizes the dependence of the CO_2 flux and hence of growth on radiation. Plotting gross assimilation as a function of radiation for a number of hourly periods in August and September showed that there was a roughly linear relation between the two below 0·5 cal./cm.^{2}/min., with evidence of light saturation above this value. At the same intensity there appeared to be more assimilation the greater the amount of cloud, i.e. the higher the proportion of diffuse radiation. This may have been because diffuse radiation penetrated the crop canopy to give a more even distribution of light than radiation received direct from the sun which may have light-saturated upper leaves leaving lower ones in deep shade.

Conclusion

Micrometeorology is a science in its infancy compared with which natural history has at least begun to mature. In this account of micrometeorology in relation to plant and animal life I have tried to show how youth can help old age. Many problems of the relationship between an organism and its aerial environment can be investigated, on the one hand by physiologists working with artificially produced climates in the laboratory, and on the other by ecologists measuring microclimate in the field. Often there is an elusive missing link between these two approaches which can be provided by the micrometeorologist. His co-operation with biological workers can extend the field of knowledge in his own science as well as in biology.

Acknowledgment

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CORRELATION OF BIOLOGICAL CHARACTERS

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During the past 60 years, biologists have become increasingly aware of the phenomenon of correlation of characters. Earlier than this, any such awareness can have been little more than subconscious, for there were no statistical tests of significance that could be applied, and even when such tests were developed there was some reluctance to use them. The first attempts to demonstrate character correlations were based on the simplest methods of analysis, the results were presented in the form of a comparison between percentages and not even the simplest of χ^2 tests was applied to them. This is in marked contrast with the present day, when methods of analysis have become so complicated that electronic computors are necessary. Not only have methods of analysis changed during this period, however, for even the concept of character correlation itself has undergone some changes, with the result that the expression has come to have different meanings to different biologists. Today there are three apparently quite different concepts, each based on a different analytical method, yet, different as they may appear to be, they are nevertheless interrelated and, in a sense, are complementary. They refer merely to three aspects of the same phenomenon.

The methods of statistical analysis that have been used to establish the occurrence of character correlations fall into two main groups, as explained by Olson & Miller (1958). The first of these involves what are known as '*Q* techniques' i.e. those designed to measure the degree of correlation between individuals on the basis of a number of characters. The second involves '*R* techniques', designed to measure the degree of correlation between characters over a number of individuals. In the first case, 'degree of correlation' implies no more than the degree of similarity, the assessment of which is the first object of any taxonomic investigation. In the past, this has always been a matter of subjective judgement, but recently there have been several attempts to make it less so by the use of these *Q* techniques. So laborious are they, however, that so far few taxonomic groups have been analysed in this way. Two most noteworthy investigations of this kind are those of Sneath (1957 *a* and *b*) on bacteria and of Michener & Sokal (1957) on solitary bees. (See also Michener, 1957, and Sokal, 1958.)

Sneath investigated the degree of similarity between a selected group of 45 strains of bacteria, among which were 38 belonging to the genus *Chromobacterium*, while the rest belonged to different genera. By means of correlation coefficients, he showed that the strains of *Chromobacterium* fell into two subgroups that differed from each other as much as any two of the remaining genera. From these observations, the idea came naturally that correlation coefficients could be used to determine when and how taxonomic groups should be split.

The work of Michener & Sokal involved the analysis of 122 characters possessed by 97 species of the genus-complex *Hoplitis*. In all, over 4500 correlation coefficients were calculated, using 'the weighted variable group method'. The results, displayed graphically, showed at a glance the degree of similarity between the various species and, as with Sneath's bacteria, the results could also be used to determine how the species could be grouped into subgenera and genera. In both cases, of course, the decision as to where to draw the line between subgroups must still be a subjective one, but undoubtedly

it is easier to make when the degree of similarity is expressed in objective terms. The development of these new techniques must surely rank as one of the most important advances that there have been in the field of pure taxonomy.

R techniques have been applied at all levels of taxonomy, ranging from individuals of a single species through species within a genus to families within even larger groups. To include all these categories in the one statement is, however, misleading for the first is so different from the rest that it warrants separate treatment. There has been a large number of investigations of individuals of single species and most of these have been of animals, of which man himself has received more attention than any other. Psychologists have been far more active than any other group of investigators in this field and have developed highly elaborate methods of multiple-factor analysis that have subsequently been used by zoologists for such characters as the measurements of the skeleton of frogs, of the skulls of squirrels and of domestic pigeons, of the bodily proportions of fossil fish and of the teeth of extinct mammals, to mention only a few. Such methods are described in the recently published book *Morphological Integration* by Olson & Miller (1958). As an illustration of the kind of character correlation that emerges from such investigations may be quoted the correlation between the length of the upper arm and the forearm of the frog and that between the femur and tibia of the frog. Correlations like this are clearly different from those shown to exist among larger taxonomic groups, though whether the difference is fundamental or merely one of degree cannot be resolved until the causal mechanisms underlying co-ordinated growth are more fully understood. It is correlations such as these that make it possible to recognize a frog or a squirrel on sight. On the other hand, correlations based on larger taxonomic groups are bound up with the concepts of primitiveness and advancement. The conviction that this is so, and that correlated characters may be indicators of evolutionary status, is one that has gained strength (chiefly among botanists) ever since 1914, when Sinnott & Bailey (1914) first demonstrated a correlation between nodal anatomy and the presence of stipules in Dicotyledons. Then followed the well-known series of papers by Bailey, Record, Wetmore, Frost, Kribs, Chattaway, Chalk and Gilbert (for detailed references see Sporne, 1956) in which correlations were demonstrated between characters of wood anatomy. Behind all this work lay the belief that, if it could be demonstrated that one character is primitive, then so are those characters that are correlated with it. Thus, if the trilacunar node can be shown to be primitive, then so must be the presence of stipules. Similarly, if long vessel elements are primitive, so must also be scalariform pitting of the vessel wall, etc.

Similar arguments have been applied to floral and vegetative characters in the Dicotyledons by Sporne (1948, 1949, 1954 a, 1954 b, 1956) and in the Monocotyledons by Lowe (1957). The statistical method used, involving merely a simple χ^2 test applied to characters taken two at a time, is relatively crude, when compared with the multiple-factor analysis described by Olson & Miller. There is no doubt that the results would have been more meaningful if more refined techniques could have been used, but when working with units as large as some angiosperm families one is limited by the form in which the information is available. Thus, it may be necessary to record any of the following statements regarding a particular character :—(i) all genera show it, (ii) most genera show it, but some do not, (iii) some genera show it, but most do not, (iv) no genera show it. These are four possibilities when the information is complete. Frequently, however, the information is incomplete and it may be necessary to record such statements as (v) some genera show the character, but there is no information about the rest, or even (vi) no information is available at all about the family. Added to these difficulties is the realization

that families vary in size from one species to many thousands of species and that characters, superficially comparable, may be fundamentally different in different families, i.e. analogous rather than homologous. Furthermore, there is the possibility that a particular character might represent a primitive condition in one family and a secondarily derived condition in another (e.g. the unisexual flower). Clearly, therefore, more refined statistical tests would be a waste of time in this work.

Table I gives a summary of the 15 characters that have so far been shown to be correlated among Dicotyledons and introduces yet a sixteenth character

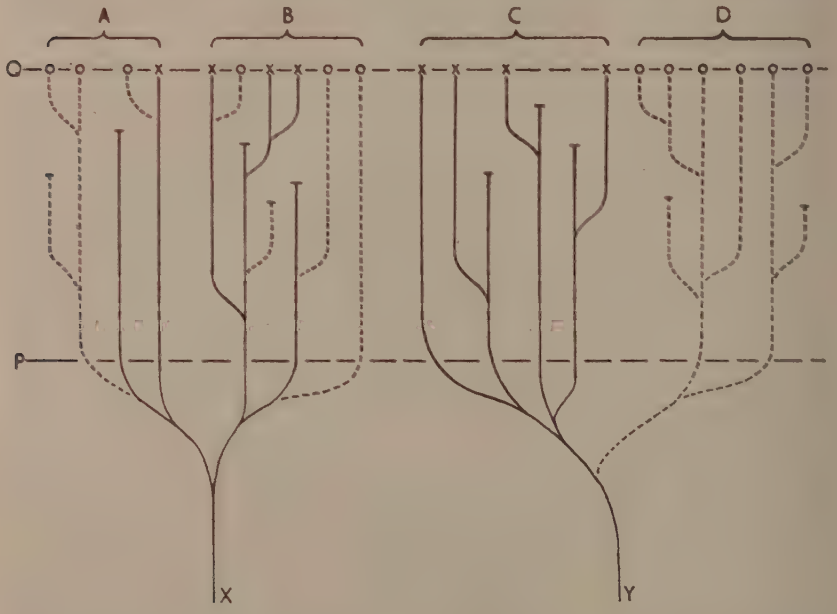
DICOTYLEDONS		15 Axile placentation	14 Carpels free	13 Nuclear endosperm	12 Integument bundles	11 Two integuments	10 Seeds arillate	9 Carpels pleiomerous	8 Stamens pleiomerous	7 Petals free	6 Flowers actinomorphic	5 Flowers unisexual	4 Stipules present	3 Leaves alternate	2 Secretory cells present	1 Woody habit		Leuco-anthocyanins
Woody habit	1	+	•	+	+	+	·:·	+	+	+	+	+	·:·	+	+			+
Secretory cells present	2	•	·:·	+	+	+	·:·	+	+	+	+	·:·	+	·:·				+
Leaves alternate	3	•	•	·:·	·:·	·:·	+	·:·	+	·:·	·:·	·:·	•					·:·
Stipules present	4	+	·:·	+	·:·	+	+	+	+	+	·:·	·:·						+
Flowers unisexual	5	•	·:·	·:·	+	·:·	·:·	·:·	·:·	·:·	+							+
Flowers actinomorphic	6	·:·	•	·:·	•	+	•	+	+	+								+
Petals free	7	+	•	+	·:·	+	+	+	+									+
Stamens pleiomerous	8	·:·	+	+	+	+	+	+										+
Carpels pleiomerous	9	+	+	·:·	·:·	+	·:·											·:·
Seeds arillate	10	·:·	·:·	·:·	+	+												•
Two integuments	11	•	+	+	·:·													+
Integument bundles	12	·:·	·:·	+														+
Nuclear endosperm	13	•	•															+
Carpels free	14																	•
Axile placentation	15																	·:·

based on the findings of Bate-Smith & Metcalfe (1957). The symbol + indicates a positive correlation significant to a probability of at least 50 : 1, the symbol ·:· represents figures that are tending towards a positive correlation, but with a lower degree of probability than 50 : 1, while the symbol ● represents a distribution equivalent to a random one, showing neither positive nor negative correlation.

Among Monocotyledons, Lowe demonstrated a high degree of positive correlation between such characters as : perianth members more numerous than five or biseriate ; perianth homoiochlamydeous ; flowers actinomorphic ; petals free ; flowers hermaphrodite ; stamens six or more ; ovary inferior ; ovules many ; endosperm cellular or helobial ; ripe pollen binucleate.

As to why there should be these groups of correlated characters, Lowe and I have both argued that they are consistent with the view that there have been

trends in the evolution of present-day organisms and that such characters are either all primitive or else all advanced. Stebbins (1951), using similar χ^2 techniques, demonstrated similar correlations within the combined group, the angiosperms, but his explanation was different. He pointed out that, while some character combinations are biologically efficient, others are less so or even impossible. Such is, no doubt, the case and this may well explain correlations between characters that are functionally connected. It might, for example, explain some of Lowe's correlations, all of which are concerned with floral characters, or some of the correlations between characters of wood anatomy, but this is unlikely to be the complete explanation and, in any case,



it does not rule out the possibility that the characters may at the same time be either primitive or advanced. Certainly, Lowe regards her characters as primitive for her findings are in accordance with those of Cheadle (1953) based on the occurrence of vessels among the Monocotyledons. It is much to be regretted that the fossil record of the Monocotyledons is so scanty, for the fossil record is the only reliable source for establishing that a group of correlated characters does represent the ancestral rather than the derived condition. The fossil record of the Dicotyledons is slighly better in this respect and suggests that the characters listed in Table I are primitive. Without this information from the fossil record, however, the decision would have been impossible. One of the most urgent tasks, therefore, is a re-examination of all fossil angiosperm material, in order that the identifications may be checked by the most up-to-date methods.

The idea that character correlations might indicate trends is not confined entirely to angiosperm-taxonomists, nor indeed to botanists, for Bell (1956) applied it in his work on the fern genus *Elaphoglossum* and Stroud (1953), working on a group of termites, demonstrated a number of correlations that

he identified with ' certain trends ' that he ' considered to be the causative agents accounting for the correlations '.

This is an appropriate moment to consider what is meant by a trend in evolution. When shorn of all metaphysical implications of ' guiding forces ', external or internal, etc. what is left is the simple statement that the proportion of organisms showing a particular character has changed progressively during the evolution of a taxonomic group. Thus, if the proportion of herbs among angiosperms is greater today than at any time during the past history of the group, then it may be said that there has been a trend towards the evolution of this character. Fig. 1 shows two ways in which this could come about. Side by side, are two hypothetical phylogenetic trees in which continuous lines represent the retention of a primitive character ' *x* ' and the dotted lines the possession in its place of an advanced character ' *o* '. For the sake of illustration, it can be assumed that among Dicotyledons ' *x* ' represents the woody habit and ' *o* ' the herbaceous. In the left-hand scheme, during the evolution of present-day organisms from the ancestor *X*, the change from woody to herbaceous has taken place several times. In the right-hand scheme, starting from ancestor *Y*, the change took place only once, a long time ago. Different as these two schemes are, yet the statistical effect is the same, for in each case the proportion of herbs at time *P* was two out of six, whereas at time *Q* (the present day) the proportion is shown as six out of ten. In each case, the proportion of herbs has increased during the time interval *PQ* and there has, therefore, been a trend towards the herbaceous habit.

Most botanists would probably visualize a trend in evolution as following the left-hand scheme, but the statistical techniques so far applied to the Dicotyledons do not make it possible to decide whether this is correct or not. However, the work of Sturtevant (1939) on the genus *Drosophila* gives hope that a combination of *Q* and *R* techniques will one day provide the answer. Firstly, by means of *Q* techniques, he made an assessment of the degree of similarity between the 42 species he was studying, on the basis of 27 characters. From this it became clear that the species fell naturally into two main subdivisions. Then by means of *R* techniques he showed that the characters used to separate these two subgroups are themselves correlated. It will readily be appreciated that these findings are more consistent with the right-hand scheme in Fig. 1 than with the left. Here the characters that distinguish subgroup *C* from subgroup *D* are ' *x* ' and ' *o* ', which are also the characters that exhibit correlations associated with evolutionary trends. By contrast, in the left-hand scheme, the characters that distinguish subgroup *A* from subgroup *B* are different from those involved in evolutionary trends, i.e. those used in *Q* analysis are different from those shown to be correlated by *R* analysis. There is hope that similar considerations may be applied to groups of organisms other than fruit flies and to groups larger than a genus.

One group that would seem to be admirable for this purpose is the leptosporangiate ferns. It is a group in which the concept of evolutionary trends is already widely accepted, and in which the direction of these trends is established by a fossil record that is more extensive than that of any other group of living plants.

Summary

During the past 60 years, there has been developed a number of statistical methods for assessing the degree of correlation between biological characters. Some of these methods have become so involved that electronic computors are necessary for their solution. The results have been used for three main purposes, the first of which is the investigation of closeness of affinity between

related organisms. The second is the investigation of the processes of co-ordination of growth among individuals of a single species, and the third is the investigation of the possible course of evolution of groups of related species, genera or families.

Investigations of the first kind have concerned bacteria and bees, and of the second, frogs, squirrels, domestic pigeons, fossil fish, fossil teeth, etc. Investigations of the third kind have been mainly in the field of botany, some covering a single fern genus, some the angiosperms as a whole, some the Dicotyledons and some the Monocotyledons. The results of this third kind of investigation are consistent with the view that trends have occurred during the evolution of present-day groups of organisms. Help from the palaeobotanist is, however, vital in establishing the correctness of this interpretation.

The meaning of the expression ' a trend in evolution ' is briefly discussed.

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A CLIMATIC PATTERN BETWEEN LATITUDES 40° AND 70° N. AND ITS PROBABLE INFLUENCE ON BIOLOGICAL DISTRIBUTIONS

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Introduction

Although important papers have been published on the effects of meteorological factors in the separation of broad vegetational types, much less work has been done on the description of distributional areas of individual plant species in terms of these factors. It is however recognized (cf. Good, 1953) that plants have temperature tolerances which differ markedly between species. For each species there is a fairly definite range of possible temperatures, and above or below these the plant will perish. Somewhere between are the optimal temperatures in which the plant will thrive best. Klages (1947) gives minimum, optimum and maximum temperatures within which each of 17 field-crop plants will grow. Thus for wheat the minimum is 37·5°–40° F., the optimum 77° F. and the maximum 86°–89·5° F. Under natural conditions of competition with better adapted plants, however it is unlikely that plants will be able to expand into temperature ranges as extreme as the ultimate possible in protected experiments.

Rainfall also greatly affects plant growth, and it is supposed that for each species there is in nature an approximately optimal rainfall level; while as a factor influencing a situation of mounting complexity, day-length also must be considered. Other meteorological factors also may have some effect, and biological areas will tend to be centred on places with optimal or nearly optimal conditions, and at such places a relative abundance of the species may be expected. In addition to the meteorological factors two other main groups of factors have long been recognized as exerting control on biological distributions: types of habitat (topography and altitude, and type, composition and structure of the soil) and biotic factors (mostly represented in competition, or one or another sort of direct or indirect attack). Good, however, considers that 'plant distribution is basically a climatic distribution. Edaphic factors can have but a secondary role . . . the difference between the two factors is best expressed by saying that while climatic factors control the extent of distribution, edaphic factors control its intensity. On climatic factors will depend whether a given species shall be a potential occupant of a given area; on edaphic factors will depend whether it will in fact occupy it, and if so in what relative abundance'.

It is not proposed in the present paper to consider the biotic and edaphic factors further, but some indication will be given of the extent to which a number of distributional areas of biological species can be reproduced in terms of four selected physical or meteorological factors. The factors used will be January and July temperatures, latitude (as controlling day-length or photoperiod), and winter rainfall. The reasons for this selection will become more apparent in the course of this paper.

Temperatures have already been mentioned as important in plant growth. Cain (1944) agreed with the principles of Good (1931) and of Mason (1936) in saying that 'climatic control is primary', 'edaphic control is secondary', and he went on to point out that 'plant geographers have long recognized this

fundamental principle in the broad parallel between temperature belts and vegetation, and in the subdivision of these belts on a moisture basis'. In the order of priority assigned to them by these authors, then, temperature and moisture are regarded as the most important factors. Of these two, temperature was the factor which Vahl (1911) considered to determine the length of the vegetation period. Blaauw and his co-workers (Hartsema, Luyten & Blaauw, 1930; Luyten, Versluys & Blaauw, 1932) have shown, for some plants, that there are different optimal temperatures for different developmental phases. Temperature would thus be important in deciding whether the conditions for these plants were optimal or not at several different stages of their development.

Moisture, which may be expressed very approximately in terms of rainfall, is the other environmental factor which has been given most consideration. Tansley (1949) considers temperature and rainfall together in his first section on the effects of environmental factors on vegetation in Britain. Hooker (1922) and Geddes (1922) in statistical papers on the yields of several farm crops, calculated their correlations against temperature and rainfall, and obtained partial correlation coefficients of much the same order against these two meteorological factors. Temperature and rainfall, as will presently be seen, are however themselves so considerably related in many parts of the world that it is at present difficult to separate their effects in plant geography.

The discovery of the importance of length of day in plant growth or flowering is comparatively recent. Murneek (1948) says 'To W. W. Garner and H. A. Allard (1920) is due all the credit for the disclosure and demonstration of the phenomenon of photoperiodism. It was a real surprise to many investigators of plant life that so "dilute" an environmental factor as length of day has so potent an effect on many plants'. Nevertheless 'According to H. A. Allard (1944) an interesting reference to the photoperiod as affecting plants is given by A. Henfrey in his book *The Vegetation of Europe* (1852) wherein a theorem is proposed that the length of day is a factor in the natural distribution of plants'.

Length of day is for practical purposes determined by latitude, and the approximate tendency for January and July temperatures to vary systematically with latitude means that variations in day-length from area to area will most often be associated with variations of these temperatures. Thus the same sort of relative difficulty which has been mentioned as probably to be encountered in any attempt to separate the effects of temperature and rainfall in plant geography will apply also in the separation of the effects of temperature and day-length.

Up to moderate altitudes at least, no other of the meteorological factors seems likely to play so generally important a part as temperature, rainfall and day-length. Wind is sometimes directly important and for some species may become the most important factor at very high altitudes, but at the moderate altitudes which will for the most part be considered in this survey it would not normally be the determining factor on plant growth, although it is recognized as a very important factor in determining precipitation. Light intensity is a function of latitude, time of year and amount of cloud (though also largely affected by density of vegetation cover) and therefore in any treatment in which latitude or a function of it is standing for day-length it must be recognized that the latitude is also introducing a light intensity factor. Length of snow cover may obviously be important to some plants, but this will broadly be a function of temperature and precipitation values, and will not be considered separately here. The number of frost-free days in the year, as indeed the numbers of days with temperatures above any arbitrarily fixed value, are also fairly closely determined when summer and winter temperatures are known.

The present investigation is a preliminary sketch of a main climatic pattern in temperate regions and its probable relationship to some biological areas. Apart from the fact that edaphic and biotic factors and some of the meteorological factors will be ignored, relationships between the remaining quantities cannot be expected to be mathematically exact for three good reasons :— (1) the available maps and data on plant areas are by no means exact, (2) meteorological data on a world scale are not exact either, and (3) as has already been indicated the problem is a very complex one, based on a large number of factors, so that although it may yield in part to simple handling it cannot wholly yield.

The intention of this paper is not, therefore, to suggest that plant areas are determined either wholly by temperatures or alternatively wholly by rainfalls and day-lengths, but rather to show that to the extent that temperatures are responsible they operate broadly in terms of the main relationship which will be adduced ; and that to the extent that rainfall and day-length are responsible a broad but distinct pattern in their operation can also be indicated.

The Present Position in Relation to the Determination of Plant Areas from Physical Data

Maps of world vegetation types, of which that given by Hayek (1926) may be taken as an example, have often been published, showing boundaries between areas of one type of vegetation and another. Vegetation types may be regarded as aggregates of individual plant species, and though the boundaries of the particular species do not usually coincide with the boundaries of the types, it is necessarily true that the meteorological or other factors which determine the areas of the species are the factors which, when the species are taken in aggregate, determine the boundaries of vegetation types. It might therefore reasonably be hoped that knowledge of the factors which determine the limits of vegetation types would give some ideas which might profitably be followed up in the discussion of plant areas. Papers by Köppen (1918) and by Thornthwaite (1931, 1933) are of interest in this connection.

After his earlier work on climate classification (1900) Köppen (1918) published a 'Classification of Climate in relation to Temperature, Precipitation and Seasonal Characteristics'. Köppen's system is not an altogether convenient one for biological purposes, since there are differences between the factors he invokes in some climates and the means of separation he uses in others, but this could perhaps be an expression of the complexity inherent in the problem itself. The main factors he uses are subdivisions of temperatures of warmest and/or of coldest months and subdivisions of summer and/or winter rainfall. Köppen did not use length of day, but his divisions of mean temperatures or of temperatures for the warmest months would fairly closely correspond with divisions of day-length.

Thornthwaite (1931) proposed a new classification which had the advantage that it was on a unified system for all areas of the world. He first applied it to North America, and later (1933) published a world map on this basis. He said 'It is understood that degree of temperature and amount of precipitation and seasonal variations of each are the most important climatic elements, but it has been recognized that the crude measurements of these elements are not satisfactory'. He then proceeded to take the same basic elements as Köppen, but used them in modified form.

For this purpose he calculated two indices, (1) a 'Precipitation Effectiveness' (P.E.) Index, based on the rainfalls and the temperatures of each month, and (2) a 'Temperature Efficiency' (T.E.) Index based on the monthly mean temperatures of the year. He used groupings *A* to *E* of the P.E. Index, representing stages of increasing aridity on a logarithmic scale, and groupings

A' to *F'* of the T.E. Index, on a similar scale, from *A'* = Tropical, to *F'* = Perpetual Frost. Combinations of these indices gave the main divisions corresponding with the most important vegetation types, but for further subdivision he found it desirable to introduce four seasonal criteria in addition, based on adequacy or deficiency of rainfall particularly in summer and winter.

Thornthwaite's P.E. Index also in effect introduces some degree of the seasonal aspect, in that a level of rainfall in winter makes a greater contribution to the Index than the same level of rainfall in summer. Seen from another angle this also means that his rainfall criterion more nearly represents winter than summer rainfall.

There is a wide gap, however, between these climatic interpretations of vegetation types and detailed description of the areas of individual plant species in terms of meteorological factors. Tansley (1949) discussing the vegetation of Britain, said 'There have been no very serious attempts ... to correlate climatic factors quantitatively with the distribution of British natural and semi-natural vegetation, and it is difficult to say how far such attempts might be successful. It may be that the interactions and complementary effects of the various factors are so complicated as to defy detailed analysis'. This does not, however, mean that the factors are not present, or are unimportant, and Turrill (1948), discussing the geographical distributions of plants, reached the general suggestion 'that the external factors controlling plant-range are far more delicately balanced than is generally supposed'.

The Biological Flora of the British Isles (1941–56) covers quite a number of species of plants in Britain, with distribution maps and a wealth of ecological detail, but it is only rarely that an isotherm is shown as corresponding with a limit of a plant distribution. The interactions of two or more isotherms were not attempted in any of this series. Thus it appears from recent material that the serious discussion of the effects of meteorological factors on plant areas is not popularly undertaken.

Hultén (1937) in his ingenious study of the present distribution of several hundreds of plant species, bases his theories almost entirely on effects of past glaciations and the subsequent spread of the plants from a limited number of refugia in which they had managed to survive, not on present-day climates.

The idea that a single isotherm might be related to one of the limits of a plant area is encountered with moderate frequency in the literature, and three examples from *The Biological Flora* will suffice by way of illustration. Woodhead (1951) gives a July isotherm as an upper temperature limit for *Lobelia dortmanna* L. ; Chapman (1950) a July or August isotherm as a lower limit for *Halimione portulacoides* (L.) Aell ; Sealy & Webb (1950) a January isotherm as a lower limit for *Arbutus unedo* L.

Elsewhere in the literature there are a few examples also of the use of two isotherms in the discussion of the boundaries of species in limited areas. Thus Werth (1927), who gave single isotherms as approximate limits for several species in Germany, pointed out that (in Germany) *Rubus chamaemorus* L. and *Montia lamprosperma* Chamisso were bounded on the south by the 63·5° F. July isotherm and in the west by the January 30·2° F. isotherm.

Limits of plant distributions in fact seem often to show some relationship with isotherms, but the latter do not in general describe the distributional limits at all adequately. However, Iversen recently (1944) brought the science of this subject an important step forward when he pointed out that 'the temperature factor is a complex one, impossible to express by means of a single cipher ; the important thing for plants is the course of the temperature during a whole year, and therefore the problem is to find the simplest expression for it'. He recalled that Vahl (1911) showed that the mean temperature for the warmest and for the coldest month together provided a good idea of the course

of the temperature during the year, and consequently also of the length of the vegetation growing period, which is of fundamental importance to a plant.

Iversen therefore chose to characterize the temperature climate by these two quantities. Using as ordinates the mean temperature of the warmest month and as abscissae that of the coldest month he went on to plot these temperatures at limiting stations for *Viscum*, *Hedera* and *Ilex* in Sweden, and draws a line through these values. On these co-ordinates he was in effect plotting small parts of the perimeters of the distributional areas of these plants.

Using practically the same factors (January and July temperatures) as co-ordinates Jeffree (1955 b) gave what was in effect an extension of this method when he approximately plotted the whole 'area' of *Ilex aquifolium* L. and of some other plants in Europe.

The Main Climatic Pattern between Latitudes 40° and 70° N.

The best known and also the most important world climatic pattern is the reduction of mean summer, and even more emphatically of mean winter temperatures from the equator towards the poles. The cooling towards the poles is not regular or exact, but this does not alter the fact that it is obviously a powerful force in the separation of boreal, temperate and tropical vegetation types. This main temperature relationship is of course primarily produced by the change of the sun's altitude.

Departures from this temperature pattern are brought about in various ways, but are dependent particularly on the movements and on the moisture-carrying capacity of the air, and positions, sizes and altitudes of the major land masses and seas, and also on the much longer days in summer than in winter towards the poles. That there are differences in temperatures which are by no means insignificant relative to the above main temperature pattern is clearly indicated by two facts :—(1) that the areas with the coldest winters in the northern hemisphere are not polar areas but an area in Siberia approximately between latitudes 60° and 70° N., about 23° from the pole, and one in Greenland at approximately 73° N.; and (2) the area with the hottest summers is not on the equator but in the Sahara desert approximately at latitude 28° N. Brooks (1956) pointed out that the warmest latitude for the year is not the equator, but latitude 10° N. It will be necessary to consider some of these departures further.

It can be no accident that in temperate latitudes there is a decided negative correlation between winter-to-summer temperature-range and rainfall, best shown with winter rainfall, for which the logarithmic values may conveniently be taken. Values of correlation coefficients will be influenced by the choice of meteorological stations, which of course are not evenly nor yet randomly scattered, but for illustration purposes some approximate correlation coefficients for every 10° latitude band, from the equator up to latitudes 75° (N. and S. combined) are shown in Table I. For latitudes 25°–64° 59′ they have been calculated from the temperatures and rainfalls recorded at all stations for which the appropriate pairs were given in the Smithsonian Collections, Volume 79 (1927), while for latitudes 0°–24° 59′ and 65°–74° 59′ the data from Volumes 90 (1934) and 105 (1947) have been included also.

It is clear from these figures that there is generally a significant correlation except in the equatorial band and in the latitudes of the main desert areas. The overall correlation for this selection of data for all these latitudes taken together is −0·28 ; but for latitudes 35°–74° 59′ it is −0·61 (for 154 d.f.). Though not enormously high, this figure, covering latitudes which are the main concern of this paper, is quite considerable, and it may therefore be said that winter rainfall in these latitudes tends to be associated with failure of the land areas to heat up in summer, or to cool down in winter, or both.

TABLE I.—Approximate correlation coefficients between winter to summer temperature range and log. winter rainfall for 10° bands of latitude

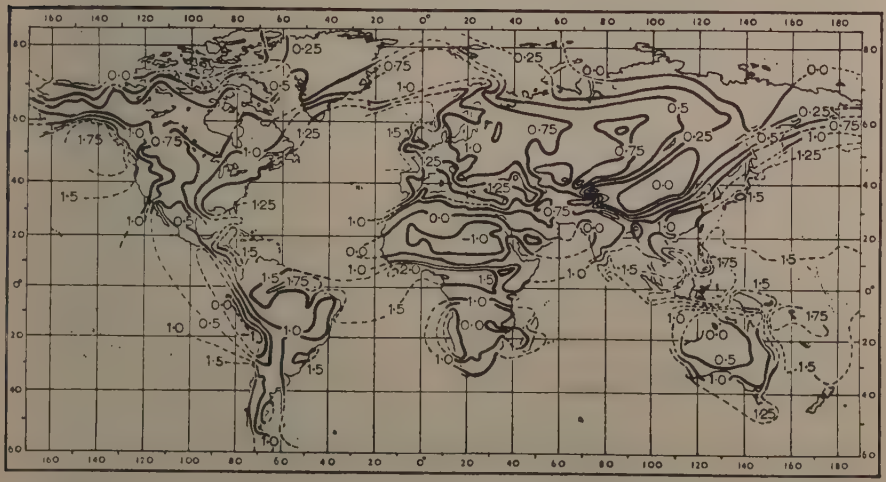
Number of stations used	Latitude range (N. and S.)	Correlation coefficient	Nominal significance
15.....	0°–4° 59′	−0·16	n.s.
49.....	5°–14° 59′	−0·56	$p < 0·001$
54.....	15°–24° 59′	−0·16	n.s.
52.....	25°–34° 59′	−0·42	$p < 0·01$
59.....	35°–44° 59′	−0·54	$p < 0·001$
52.....	45°–54° 59′	−0·56	$p < 0·001$
25.....	55°–64° 59′	−0·74	$p < 0·001$
20.....	65°–74° 59′	−0·52	$p < 0·05$

The water which drains away by the river systems from the land masses to the sea has all to be brought back again in the air and precipitated, usually as rain or snow ; and in this transfer of water from the seas to the land two important factors operate. (1) The moisture-carrying capacity of the air rises steeply with its temperature, so that more water is carried, and there is therefore potentially more opportunity for rainfall in equatorial regions than near the poles, and it would in fact be correct to speak of a marked tendency towards a general world pattern of maximum rainfall near the equator and reduced precipitation towards the poles both in summer and winter if the latitudes of the main desert areas were left out of account, for in these latitudes there is a major inversion of this pattern, which will be discussed later. (2) Particularly in winter, the moisture tends to be precipitated in greater measure relatively near the coasts than far inland, partly because any cooling of the air and consequent precipitation which occurs near the coasts represents a reduction in the moisture of the air which proceeds inland. Thus the areas near the west and to a lesser extent the east coasts of both North America and Eurasia receive generally much higher rainfall than far inland. The prevailing wind direction plays an important part in this.

The main distribution of rainfall is from the present point of view most easily seen in summer and winter isohyets scaled in logarithmic units, which are given in Figs 1 and 2. (These were drawn up from log. rainfalls calculated for 765 stations. Sources of data and other details are given by Jeffree, 1957.) Moisture-laden air, when it rises is cooled by adiabatic expansion and therefore its water-carrying capacity is reduced, and precipitation becomes more probable. Air masses are lifted by mountain ranges, which therefore influence rainfall. Air masses are however also rising where winds from two opposite directions meet, and an important world pattern of this sort must be briefly considered. The dominant wind systems established by the rotation of the earth show areas of opposing north-easterly and south-easterly winds at the equator, and the up-current where these meet is a major factor in the very high equatorial rainfall. About 20°–30° from the equator on either side, however, is a zone of the opposite sort, from which air is proceeding both north and south and supplying these equatorial trade-winds and the dominant south-westerlies of the temperate regions of the northern hemisphere, or north-westerlies of the southern hemisphere. Here the air masses are descending, are in consequence adiabatically heated, and a relatively rain-free zone results. Thus the crude overall pattern of rainfalls from the equator to the poles shows an equatorial band of high rainfall reducing to a low level at about 20°–30° N. and S. latitudes, subsequently rising somewhat, and then falling again towards the poles. This

FIG 1. LOG_{10}. (SUMMER RAINFALL, INCHES).

FIG. 2. LOG_{10}. (WINTER RAINFALL, INCHES)



overall pattern of rainfall is however very greatly further modified by distance from the sea, and also by other factors particularly of wind directions, sea temperatures, and mountain ranges.

While the climate of the world as a whole therefore shows a marked correlation between rainfall and temperature ranges, and also a fairly general reduction of temperature from equator to poles, and in addition a reduction of rainfall with latitude in many areas, the very strong tendency to inversion to very low rainfalls and high summer temperatures at about the latitudes of the main hot desert areas introduces a major complication into any attempt to present a single meteorological discussion for the whole world in anything like simple terms. Beyond latitude 50° N. and to some extent beyond 40° N. the traces of this complication have largely been passed, and the areas nearer the poles have more nearly a single trend with increasing latitudes, though modified greatly by the reducing precipitations and increasing winter-summer temperature ranges with increasing distance from the sea.

For this reason the discussion which follows will for the most part be confined to the approximate latitude band 40°–70° N., and is not intended to apply outside this band.

The influence of the sea on the temperatures of the adjacent land is obviously very marked, and extends inland for many hundreds of miles from the west coast of Eurasia, and from the east and west coasts of N. America. Yet clearly this is not a direct warming or cooling of the land by the sea, an influence which for physical reasons could not extend very far. It is mostly an influence through the agency of air movements from the sea over the land. Such influence is partly direct, as the direct warming action of air passing over the Gulf Stream on to parts of the European coast. It is also partly a direct effect of precipitation, which cools the land in summer. It is however to a large extent a question of the heat conserving effect of cloud and haze cover which protects these areas from loss of heat in winter and also from the receipt of all the possible heat from the sun in the summer. This effect is much greater near the coasts than far inland.

The heat-conserving effect of moisture-laden air operates between day and night as well as between summer and winter, and it is broadly true that at any given latitude the pattern of increasing diurnal temperature range with distance from the sea (which is shown by Shaw, 1928, pp. 84 and 85) is rather similar to that of increasing annual temperature range.

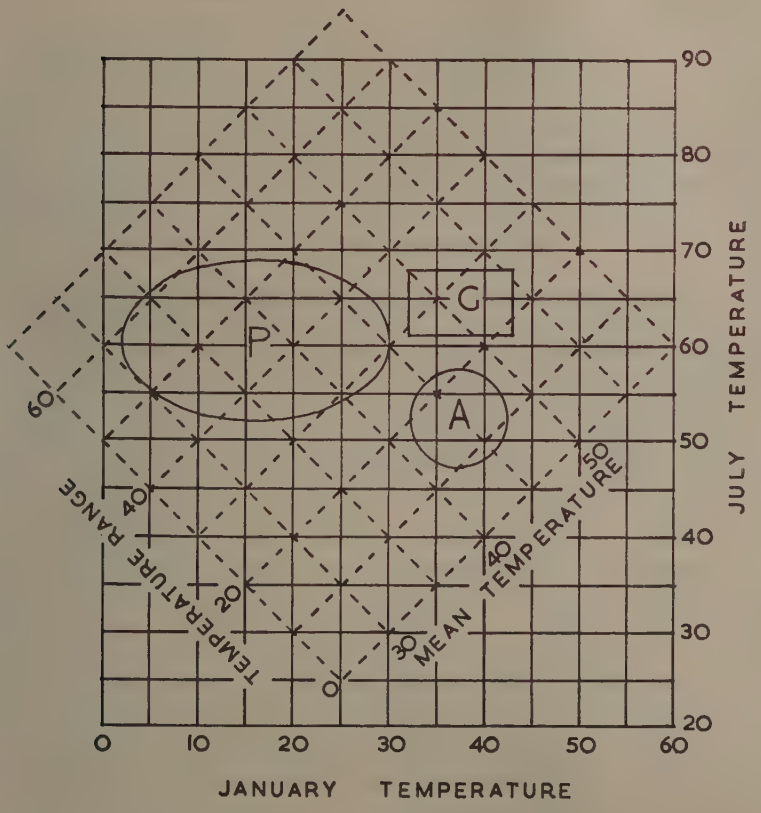
It has been indicated already that the increasing annual mean temperature between the tropics and the poles undoubtedly affects vegetation patterns. Annual mean temperature is not, however, a good measure of the influence of temperatures on plant or animal life (Vahl, 1911). Irkutsk in Siberia, for example, with January and July temperatures —4·8° and 63·2° F. respectively has practically the same annual mean temperature as Säntis in Switzerland, with January and July temperatures 16·5° and 40·3° F. The temperature ranges of these two places are respectively 68·0° and 23·8° F. Areas selected as similar on a basis of both summer and winter temperatures independently are for such reasons obviously likely to be much more nearly similar as habitats for living organisms than areas selected on annual mean temperatures alone.

Co-ordinates of January and July Temperatures and of Mean Temperature and Temperature Range

Within latitudes 40°–70° January is usually the coldest and July the warmest month, and the annual mean temperature is also rather closely related to the mean of the temperatures for January and July. An examination of Fig. 3 (diagrammatic) will show that an area such as the circle *A* which may be defined in terms of January and July temperatures in reference to the main

co-ordinates of the figure may equally be defined in just the same way by mean temperature (mean of January and July) and temperature range (difference between July and January temperatures) in reference to the inclined system of co-ordinates. Indeed these co-ordinates nearly define the 'course of temperature during the whole year', which was Iversen's criterion and reason for using temperatures of warmest and coldest months.

FIG. 3. JANUARY AND JULY TEMPERATURES, MEAN TEMPERATURE, AND TEMPERATURE RANGE.



This sufficiently exact relationship is shadowed by an interesting very approximate relationship. Since annual mean temperature isotherms (Shaw 1928, pp. 80–81, or many atlases) tend to run usually somewhat parallel with lines of latitude, while log. winter precipitation tends to be considerably correlated with temperature range, areas with equal January and July temperatures exhibit some tendency to be rather near to areas of equal latitude and winter rainfall.

Symbols, and Sources of Meteorological Data

The temperature data used in drawing up the maps which follow are taken directly from isotherm maps given in *The Great Russian Atlas* (Central Hygrometeorological Department, Moscow, 1939). The precipitation data are from the isohyet maps given by Jeffree (1957), shown in Figs 1 and 2 above.

The following *symbols* will be used in the keys and titles to the maps :—

ϕ = latitude.
α = January temperature (July in S. hemisphere).
γ = July temperature (January in S. hemisphere).
(The above temperatures, in degrees F., will be actual monthly mean temperatures unless otherwise stated.)
ν = $\log_{.10}$ (winter precipitation, inches).
(Winter precipitation is from November to April, inclusive, in the N. hemisphere, May to October in the S. hemisphere.)

Areas with a Progression of January and July Temperature Limits

It has been said that annual mean temperature is not likely to provide a very adequate criterion of the flora of an area because of the many different values of January and July temperatures which it may represent. It is instructive, approximately between latitudes 40° and 65°, to consider the geographical areas corresponding with a representative series of January and July temperature limits.

In Figs 4 and 5 such areas have been drawn up on a basis of January and July sea-level reduced isotherms. (Isotherms reduced to sea-level have been used in the preliminary treatment represented in these two figures, to avoid the complications of small details. 'Actual' isotherms were however used in the preparation of subsequent maps.)

The main features of the pattern presented by these two figures, which together show seven different climatic ranges based on temperatures, are due chiefly to changes in January temperature, rather than to the relatively unimportant changes in July temperatures which it has been convenient to adopt.

In Fig. 4, *A*, *B*, *C* and *D* represent a series of areas with increasing limits of January (and also of July) temperatures, the January temperatures for area *A* already being very low (−33° F. to − 8° F.). In these latitudes such areas of very low winter temperatures are found in the far east of Asia and nowhere else, so that there is no wide choice in the site for the first area, *A*, of this series. *A* is well to the east rather than in the centre of Eurasia (an effect of the westerly element in the prevailing wind). Successive temperature-areas with wider ranges in particular of January temperature spread out towards the east and west coasts, but reach the former first. In N. America the area *A* is not represented at all, area *B* is almost central between the coasts, and areas *C* and particularly *D* show an interesting inclination from high latitudes in the west to lower latitudes in the east.

In Fig. 5 areas *D*, *E*, *F* and *G* show a series starting from the same area *D* (with a great range of January temperatures and stretching right across Eurasia) and proceeding once again to progressively narrower ranges of January limits, but this time in the direction of high rather than low winter temperatures. In Eurasia a split has already occurred in the areas *E*, there being a large westerly and a smaller easterly area. In *F* the areas are smaller, particularly that in the east, while *G* is unique to the west coast, the equivalent eastern area being over the sea. In N. America the division is not at first complete, and the final area *G* is very small in the west, and is again represented only by a sea area in the east.

These two figures give a fairly complete understanding of the broad aspects of the main possible climates as defined by temperatures in this latitude band, and it can readily be appreciated that intermediate limits could have been chosen. The only main feature which has not been clearly brought out is that with winter temperature limits which may be selected to extend neither to the cold centre nor to the coasts, it is also possible to obtain areas which are inland on either side of the continental masses, but which do not join up in the centre. This is particularly possible at somewhat lower latitudes in North America. In Eurasia the easterly components of such pairs tend to be very small, or sometimes to disappear, but quite characteristic non-coastal but not central temperature-areas can be selected inland from the west coast. There are of course also modifications of detail in the areas selected with changes in the July temperature band (which broadly corresponds with the latitude band), and there are other minor points of detail in the areas which need not at present be discussed.

This is not therefore a detailed exposition of the possible areas, but it does illustrate that temperature specifications, if based on January and on July limits separately, divide these latitude ranges up in very characteristic ways.

In the southern hemisphere there is very little land strictly within these latitudes, but there are relatively small areas corresponding with some of these temperature limits in South America and New Zealand. There will be no need at present, however, to discuss in detail the temperature patterns over these areas.

Areas with a Progression of Latitude and of Winter Rainfall Limits

In Figs 6 and 7 areas in approximately the same latitudes have been chosen on the basis of latitude limits and limits of winter rainfall. In the general pattern obtained, the precipitation rather than the latitudes are the important factor.

In Fig. 6 area *A* is selected as having the lowest limits of winter rainfall. It inevitably comes in eastern Siberia, and, as has been seen to be the case with the roughly corresponding nearly extreme temperature specification, there is no corresponding area in North America. Areas *B*, *C* and *D* have progressively greater ranges of winter rainfall, the last again spreading virtually the whole way across the two continents.

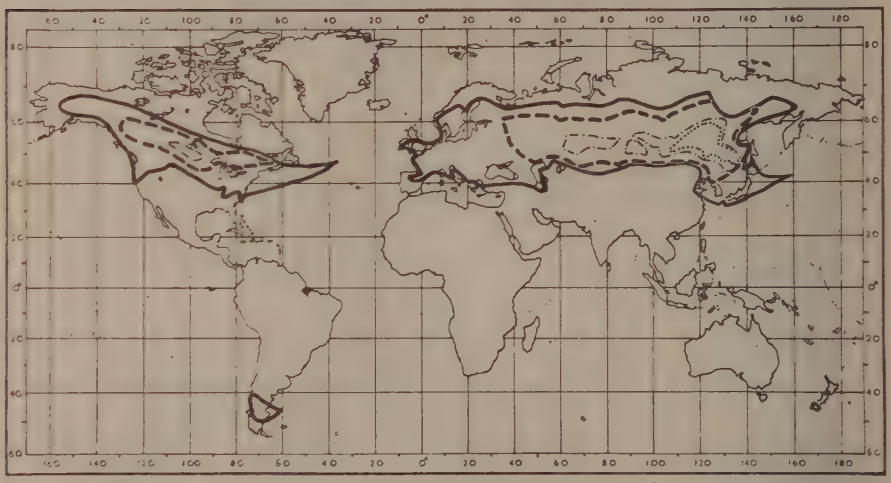
In Fig. 7, from *D* to *G* the rainfall limits are progressively reduced again, but this time in the direction of the wettest specifications only. Again a split into easterly and westerly areas occurs in the two continents, and again the final area *G* occurs in west Eurasia but not in the east (except in the sea), though this time it does have small representatives near both coasts of N. America. The areas are once again much more symmetrically placed in N. America than in Europe.

Just as was the case in the temperature specifications, Figs 6 and 7 again give a broad key to the main characteristic winter-rainfall areas which might be selected in these latitudes, and while it certainly is not possible to select rainfall and temperature values in such a way as to make the two sets of maps agree exactly, it is perfectly clear that the two sets of criteria used respectively in Figs 4 and 5 and in Figs 6 and 7 are making the broad selection of areas on the same essential main pattern.

Equiformal Climatic Areas (in short ECAs)

Attention has been drawn above to the main features of a strongly marked climatic pattern between latitudes 40° and 70° N., and it may reasonably be supposed that if plant distributions are at all affected by temperatures and/or

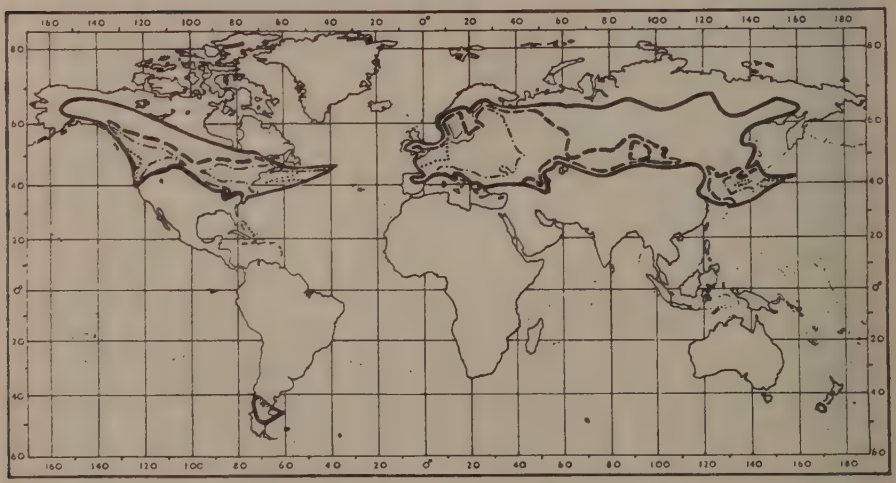
FIG. 4. CLIMATES BASED ON JANUARY AND JULY TEMPERATURES.



"A" ..... α -33° to -8° γ 68° to 72°
"B" -·-·- α -42° to 3° γ 67° to 73°
"C" – – – α -44° to 14° γ 63° to 77°
"D" —— α -44° to 43° γ 59° to 79°

(IN °F. REDUCED TO SEA LEVEL)

FIG. 5. CLIMATES BASED ON JANUARY AND JULY TEMPERATURES.



"D" —— α -44° to 43° γ 59° to 79°
"E" – – – α 3° to 43° γ 61° to 78°
"F" -·-·- α 14° to 43° γ 61° to 74°
"G" ..... α 32° to 43° γ 61° to 68°

(IN °F. REDUCED TO SEA LEVEL)

rainfalls they are likely to be considerably influenced by features of this broad pattern.

Discussing plant areas Hultén (1937) bases practically the whole of his description on 'equiformal progressive areas' which are a number of areas of which the smallest is at some geographical location which is referred to as the 'centre', and the others, of progressively larger sizes, spread out further from the centre in some or in all directions, not necessarily uniformly, but forming a fairly obvious series. He finds it possible to group very large numbers of plant areas into such series, and he enumerates the positions of the several necessary centres. He regards the centres as refugia, that is, places which were not covered with ice during the maximum Pleistocene glaciation. Elaborating this theme he says, 'All plants of our area radiate from districts that were not completely buried under the ice-sheet of the maximum glaciation. In other words :—the plants have spread over the arctic and boreal belt from the refugia close to the ice, where they were left in possession of a small part of their earlier area, and where they were able to survive the severe conditions of the maximum glaciation'. In this book, however, he makes no suggestion that the areas which he has recorded might possibly be explained in any important degree on a basis of present climates alone.

Without the necessity of implying any relationship with plant areas, it may however now be noticed that it would be legitimate to coin a phrase from Hultén and speak of 'equiformal progressive climatic areas' which could be specified in purely meteorological terms. These could be centred on some small area with a limited range to its meteorological specification, while the progressive areas could be obtained by progressively increasing the meteorological limits of the specification. Various different meteorological factors might be chosen, but this could for instance be done in relation to present-day January and July temperatures, or in relation to rainfalls and latitudes.

This is, however, exactly what has been sketched out in Figs 4–7 and in the previous discussion, so that these figures may be regarded as showing respectively 'equiformal areas of January and July temperatures', and 'equiformal areas of latitude and winter rainfall'. These ECAs have been drawn in rather wide steps, but clearly it would be equally possible to draw tidier series with a larger number of areas separated by smaller gradations.

Other such ECAs could be drawn, depending on the specification adopted as a starting point, and the manner of expansion adopted. However, for reasons which have already been advanced, it may be said that Figs 4–7 represent apparently the most important as well as the most typical ECAs of this latitude band.

Comparison with Equiformal Plant Areas (EPAs)

In order to compare these ECAs with EPAs it will now be convenient to consider the first example of EPAs given by Hultén (1937, Hultén's Fig. 1). These consist of five areas, the smallest centred on eastern Siberia and the largest spreading practically the whole way across Eurasia. Four of them are reproduced as an expanded series (continuous heavy lines) in Figs 8–11. It is immediately apparent that they form a series basically very similar to series *A* to *D* in Figs 4 and 6. In fact there is every indication that they correspond in essential features with the first example of ECAs. (The fifth area in this series of Hultén's has been omitted from this paper from considerations of economy in illustrations. It is for the plant *Carex globularis* L. and is substantially intermediate between Figs 10 and 11, showing no special features.)

The Manner of Specification of Climatic Areas

Turning again to Figs 4 and 5, areas were there chosen each with two limits of

FIG. 6. CLIMATES BASED ON LATITUDE AND WINTER RAINFALL.

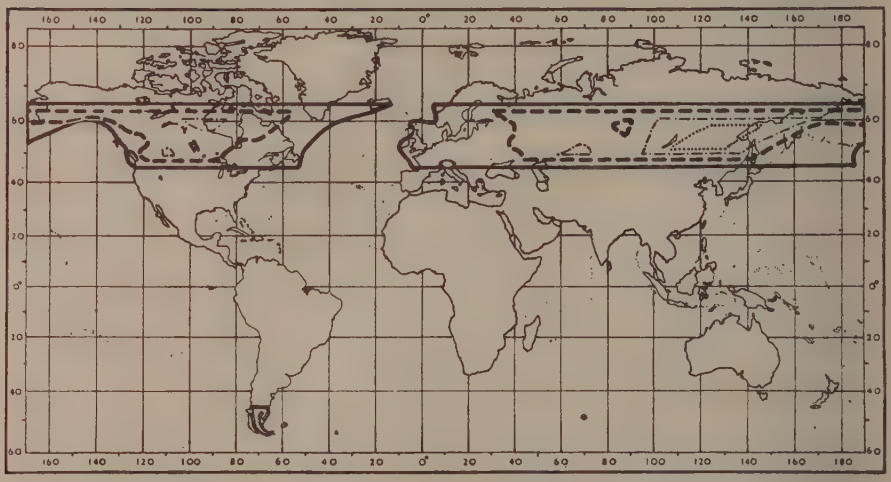


FIG. 7. CLIMATES BASED ON LATITUDE AND WINTER RAINFALL.

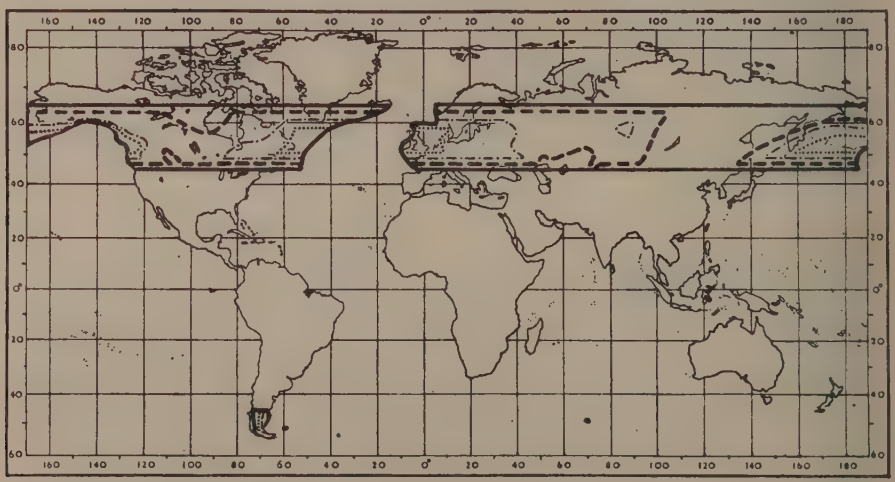
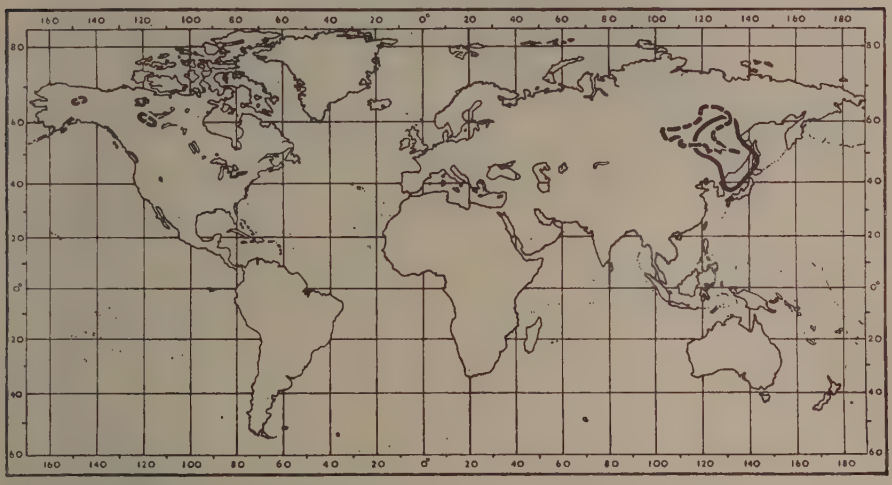


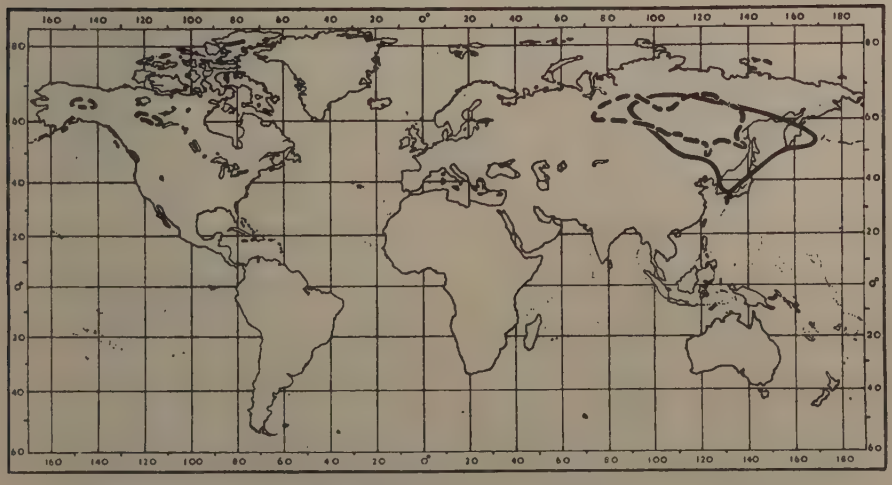
FIG. 8 DISTRIBUTION OF SMILACINA DAHURICA AND AREAS BASED ON VALUES OF α AND γ.



——— DISTRIBUTION AFTER HULTÉN (1937)

– – – AREAS BASED ON α = -44° to -10°F. γ = 60·5° to 66·5°F.

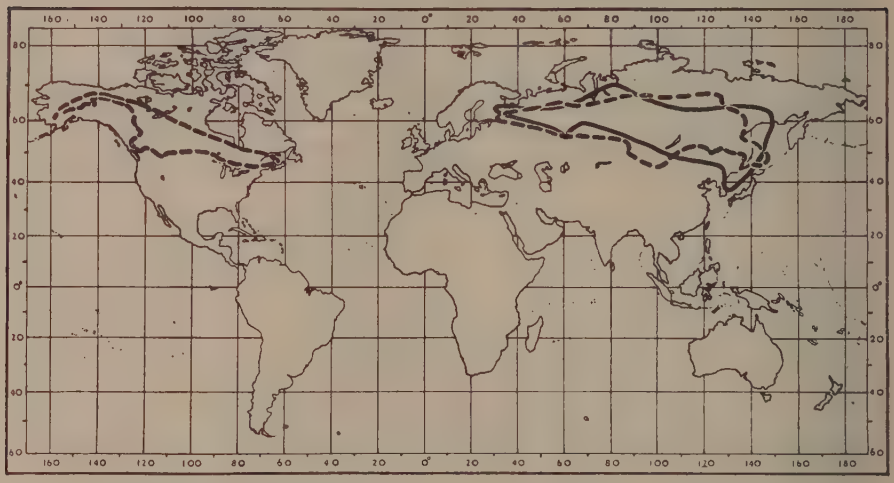
FIG. 9. DISTRIBUTION OF STELLARIA RADIANS AND AREAS BASED ON VALUES OF α AND γ.



——— DISTRIBUTION AFTER HULTÉN (1937)

– – – AREAS BASED ON α = -58° to -10°F. γ = 56° to 65°F.

FIG. 10. DISTRIBUTION OF RUBUS HUMULIFOLIUS AND AREAS BASED ON VALUES OF α AND γ.



——— DISTRIBUTION AFTER HULTÉN (1937)

– – – AREAS BASED ON α = -60° to 15°F. γ = 54° to 66°F.

FIG. 11. DISTRIBUTION OF MAIANTHEMUM BIFOLIUM AND AREAS BASED ON VALUES OF α AND γ.

——— DISTRIBUTION AFTER HULTÉN (1937)

– – – AREAS BASED ON α = -60° to 41°F. γ = 50° to 70°F.

January and two limits of July temperatures. These temperature limits could also be shown on the co-ordinate system used in Fig. 3. Area *G*, Fig. 3, is in fact a plot on these co-ordinates of the corresponding Area *G* in Fig. 5.

This is a perfectly good area from the human point of view of a climate specification, but if it were imagined to represent the temperature limits of a plant area and it were supposed that these temperatures were the factors mainly determining the area, it would then seem surprising if for one part of the boundary the 68° July temperature were the operative factor, and then suddenly it entirely ceased to be operative, and the 32° January isotherm became the sole effective factor. It would be much more probable that there should be a gradual change-over in the operation of two such factors. Such a gradual change-over would be represented by a rounding of the corners of the rectangular area shown for *G* in Fig. 3.

Cain (1944) in his recapitulation of the principles of plant geography, says 'Ranges of plants are limited by tolerances', and 'The environment is holocoenotic'. If such a factor as summer (or July) temperature plays a part in the survival of a plant species, the simplest of the possible assumptions is that there would be an optimum value of summer temperature and that survival would occur within a temperature band, with this optimum somewhere within the band. A similar first assumption might be made about another factor, such as winter (or January) temperature. These two bands would then represent the tolerances of the plant in these respects. The term 'holocoenotic' however indicates that if several factors are operating, the plant responds to the combined effect of all of them, and not to one alone. If then one factor, perhaps July temperature, is at its optimal value, the effect of a nearly critical value of January temperature would not be so disastrous as it would if July temperature were also nearly critical. If the effect of the factors were not holocoenotic the area of a plant on Cartesian co-ordinates might in fact be a rectangle. If the environment is holocoenotic, the picture of the meaning of this conception is that the corners of the rectangle become considerably rounded off.

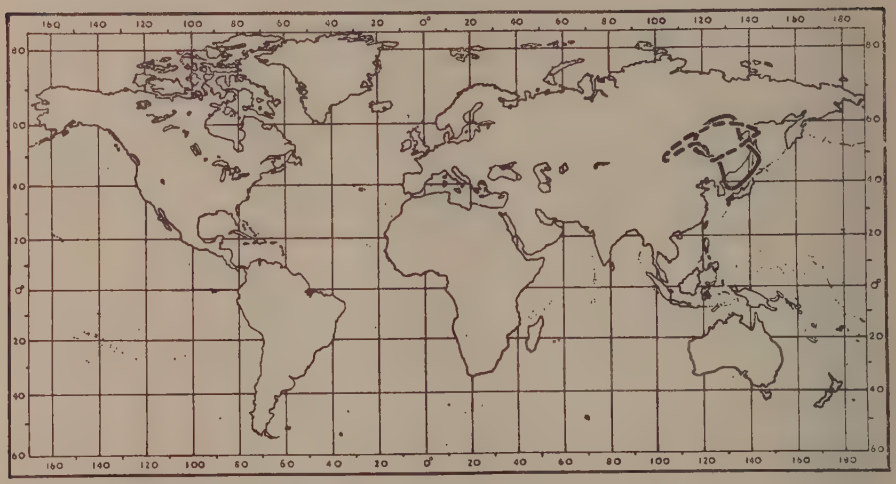
Just how much and in what way they should be 'rounded' would depend on the exact laws of decline of plant population with departures of temperatures from the optima, which are not known ; but the assumption that the rectangle becomes an ellipse, while it certainly cannot be expected to be exactly right (for reasons which will not be examined at present) is a more reasonable assumption than imagining it to be a rectangle.

For the above reason, in attempting to give areas based on January and July temperatures, in Figs 8–11, and based on latitudes and log. winter rainfalls in Figs 12–15, to correspond with the areas of Hultén's Fig. 1, and in subsequent figures to correspond with other biological distributions, the limits plotted will not be those which would represent rectangles on Cartesian co-ordinates, but ellipses. These will for the present be selected with their axes parallel with the α, γ, ϕ and ν axes respectively, as the case may be. The area *P*, Fig. 3, is such an ellipse, corresponding with the limits α=2°–30°, γ=52°–69° F., and is in fact the plot on these Cartesian co-ordinates of the area for *Picea abies* (L.) Karst. (= *P. excelsa* Link) in the map given by Jeffree (1955 b).

Climatic Limits Corresponding with Hultén's First Group of EPAs

It has already been shown that something broadly similar to this set of EPAs can be represented by either of two alternative series of ECAs. The above use of elliptical areas in a plot on Cartesian co-ordinates will now be used as a minor reasonable refinement of plotting, in an attempt to reduce one obvious probably source of error in the climatic areas specifications. The limits chosen

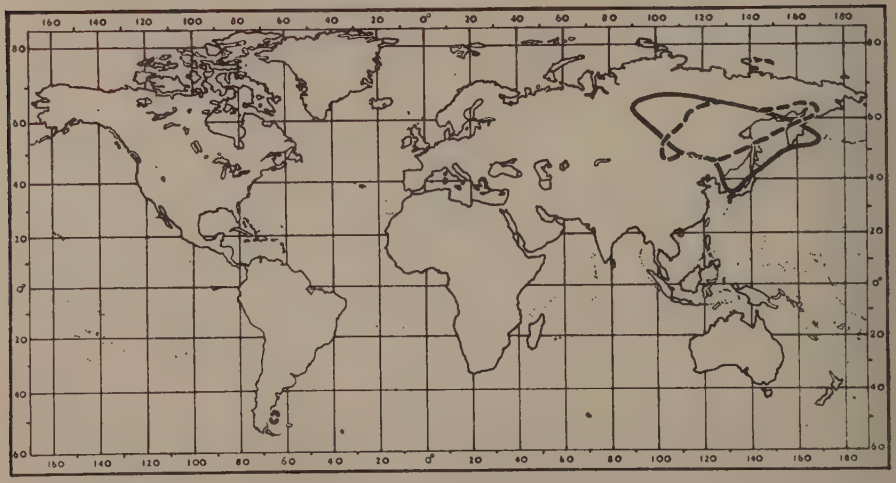
FIG. 12 DISTRIBUTION OF SMILACINA DAHURICA AND AREAS BASED ON VALUES OF ϕ AND ν.



——— DISTRIBUTION AFTER HULTÉN (1937)

– – – AREAS BASED ON ϕ = 48° to 60° ν = 0 to 0·35

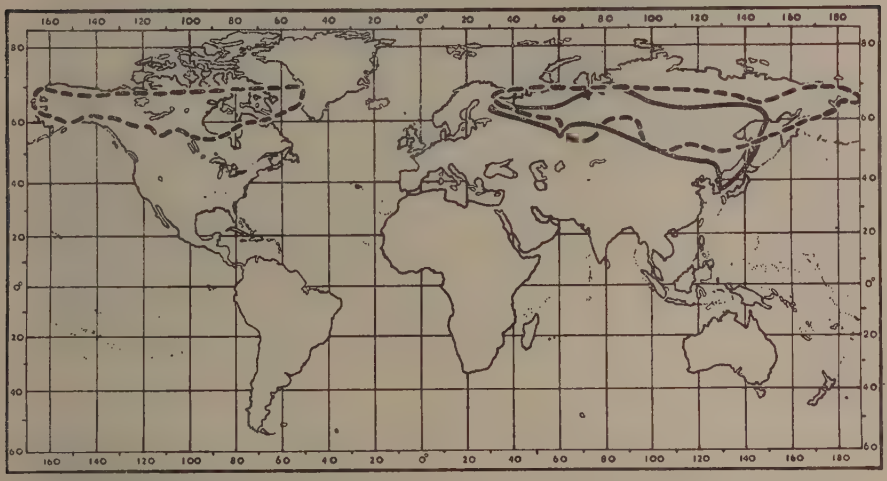
FIG. 13. DISTRIBUTION OF STELLARIA RADIANS AND AREAS BASED ON VALUES OF ϕ AND ν.



——— DISTRIBUTION AFTER HULTÉN (1937)

– – – AREAS BASED ON ϕ = 47° to 65° ν = −0·25 to 0·55

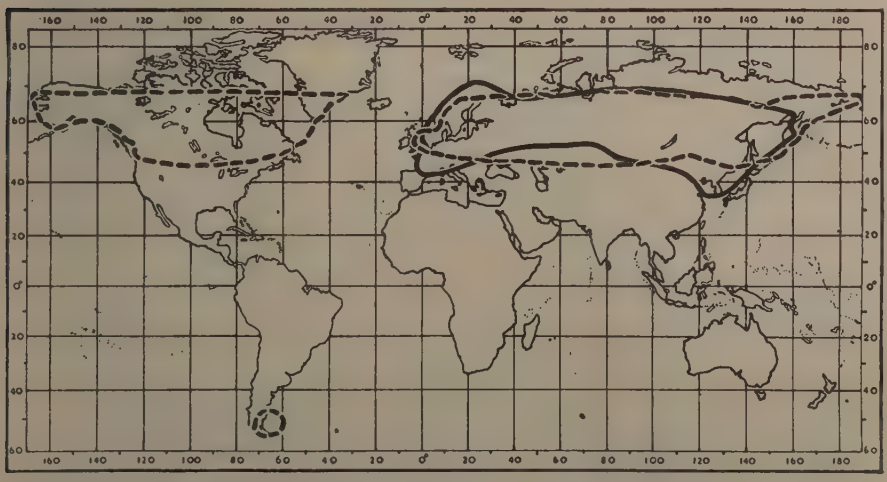
FIG. 14. DISTRIBUTION OF RUBUS HUMULIFOLIUS AND AREAS BASED ON VALUES OF ϕ AND ν.



——— DISTRIBUTION AFTER HULTÉN (1937)

– – – AREAS BASED ON ϕ = 50° to 70° ν = −0·25 to 0·8

FIG. 15. DISTRIBUTION OF MAIANTHEMUM BIFOLIUM AND AREAS BASED ON VALUES OF ϕ AND ν.



——— DISTRIBUTION AFTER HULTÉN (1937)

– – – AREAS BASED ON ϕ = 46° to 69° ν = −0·3 to 1·3

will not be the crude steps used in Figs 4–7, but will be selected to correspond as closely as possible with the areas given by Hultén.

Figs 8–11 show in the bold dotted lines areas, roughly corresponding with Hultén's areas, plotted in this way against α and γ, and Figs 12–15 show them plotted against ϕ and ν. It will be seen that the areas obtained with the two different sets of co-ordinates are in many respects similar, and both apparently show considerable relationship with the plant areas. The relationship with the temperature co-ordinates is not very exact in the case of the smallest area (*Smilacina dahurica* Turcz.) although the temperature criteria do mark out as unique in the northern hemisphere an area which overlaps with the given plant area. It could however be said that neither the botanical nor the meteorological data on which these two areas depend are likely to be very exactly recorded in Siberia. The relationships with these temperature co-ordinates improve as the areas in the series become larger. With the latitude and log. winter rainfall co-ordinates the agreement in the case of the smallest area is as good or better, but as the largest (*Maianthemum bifolium* (L.) F. W. Schmidt) is approached the results are not so good. In addition to the areas in Eurasia it is to be noted that the corresponding American areas on the two systems agree, not in detail, but to a very marked extent.

Further Examples of Areas Related to the Cold Dry-winter Centres Within the Continents

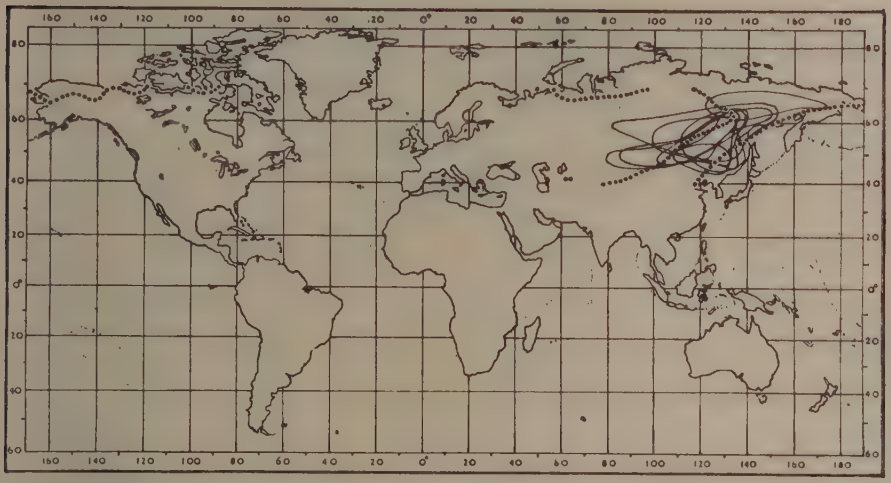
In addition to the example given above, Hultén (1937) gives 41 other plates of EPAs. It is not possible to reproduce all these plates in the present paper, but in many of them there is evidence of arrangements which show broad but unmistakable similarities—that is, which have a centre apparently closely related to this area of the coldest winters for Eurasia, and with equiformal areas spreading almost or right across the continent. These are Hultén's Plates 2, 3, 4, 5, 6, 7, 10 and 33, covering (with Plate 1) 593 plant species. In Fig. 16 the central areas of all these nine plates are shown superimposed, together with (dotted lines) the 0·25 log. winter rainfall isohyets between latitudes 40° and 70° N. Some of the centres are further north than others, but the positions seem very definitely related to the main band of lowest winter rainfall which runs in a NE and SW direction about 20° of latitude west of the east coast of Eurasia.

Fig. 17 similarly shows superimposed the most extreme limits given for the same nine series of EPAs, with (dotted lines) the 1·25 log. winter rainfall isohyets between the same latitudes. In this way the evident tendency for these EPAs to extend both in the westerly and easterly directions from limits of lowest to limits of highest rainfall is brought out. The same tendency could alternatively have been expressed as a series of extensions from the area of high summer-winter temperature range to areas of low temperature range.

Others of Hultén's plates represent equally good examples of the same relationship in the N. American continent. These are his Plates 11 and 12, together representing 75 species. His Plate 21 shows as the central area an area closely similar to Area *C* in Fig. 4 of the present paper, and his Plate 18 centres on a similar area further south. His Plate 36 uses a similar area in N. America together with a broadly corresponding area almost the whole way across Eurasia. All of these are essentially similar examples and represent a further 136 species. (This however must not be taken as implying that all of the above examples could with equal success be reproduced in detail from temperature or from latitude and rainfall data.)

Fig. 18 of the present paper shows the above type of inclined area across N. America in the case of *Pinus banksiana* Lamb. (Area after Munns, 1938). A corresponding area obtained in the manner indicated from January and July

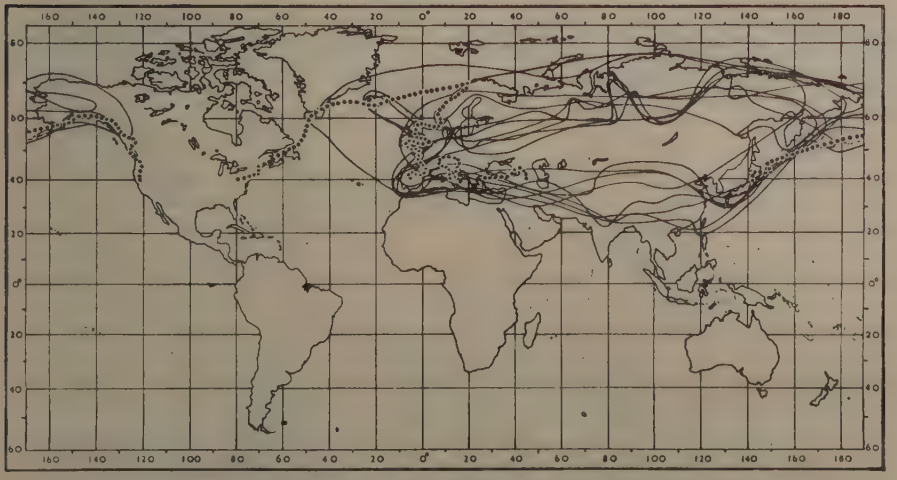
FIG. 16. CENTRAL AREAS OF NINE OF HULTÉN'S PLATES, AND REGIONS OF LOW WINTER RAINFALL.



——— CENTRAL AREAS AFTER HULTÉN (1937), PLATES 1, 2, 3, 4, 5, 6, 7, 10 and 33.

..... $V = 0{\cdot}25$, between $\phi = 40°$ and 70° N.

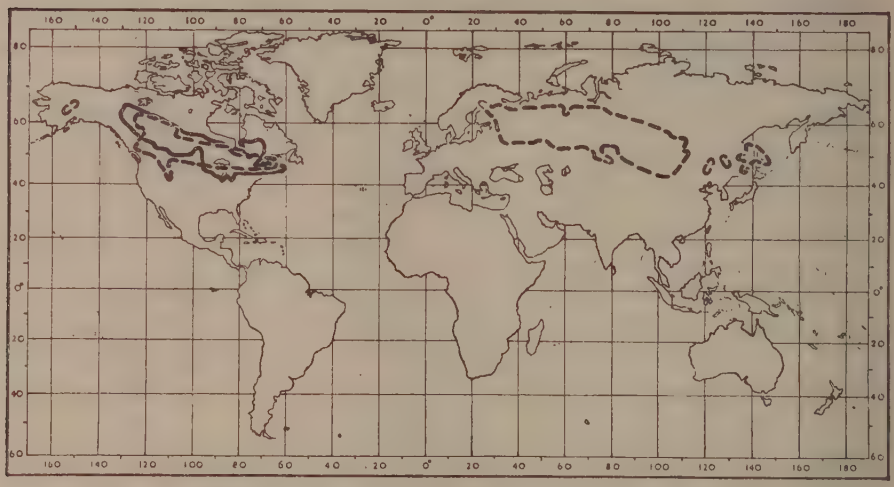
FIG. 17. LARGEST AREAS OF NINE OF HULTÉN'S PLATES, AND REGIONS OF HIGH WINTER RAINFALL.



——— LARGEST OF EQUIFORMAL AREAS AFTER HULTÉN (1937), PLATES 1, 2, 3, 4, 5, 6, 7, 10 and 33.

..... $V = 1{\cdot}25$, between $\phi = 40°$ and 70°N.

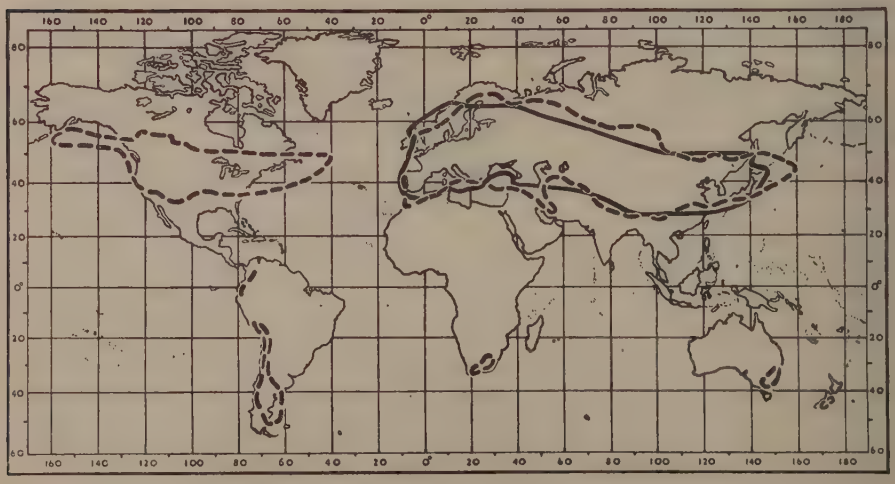
FIG. 18. DISTRIBUTION OF PINUS BANKSIANA AND AREAS BASED ON VALUES OF α AND γ.



——— DISTRIBUTION AFTER MUNNS (1938)

– – – AREAS BASED ON α = -22° to 18°F. γ = 56° to 69°F.

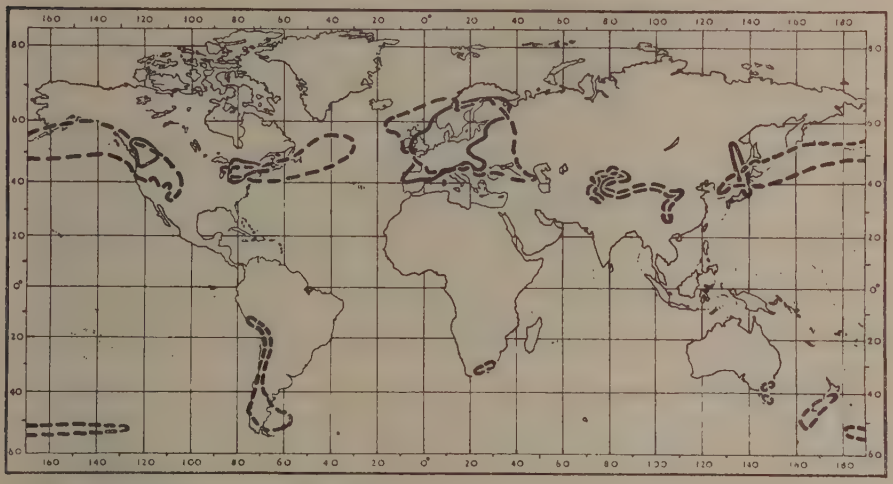
FIG. 19. DISTRIBUTION OF BUFO BUFO AND AREAS BASED ON VALUES OF α AND γ.



——— DISTRIBUTION AFTER BOULENGER (1898).

– – – AREAS BASED ON α = -13° to 48°F. γ = 54° to 82°F.

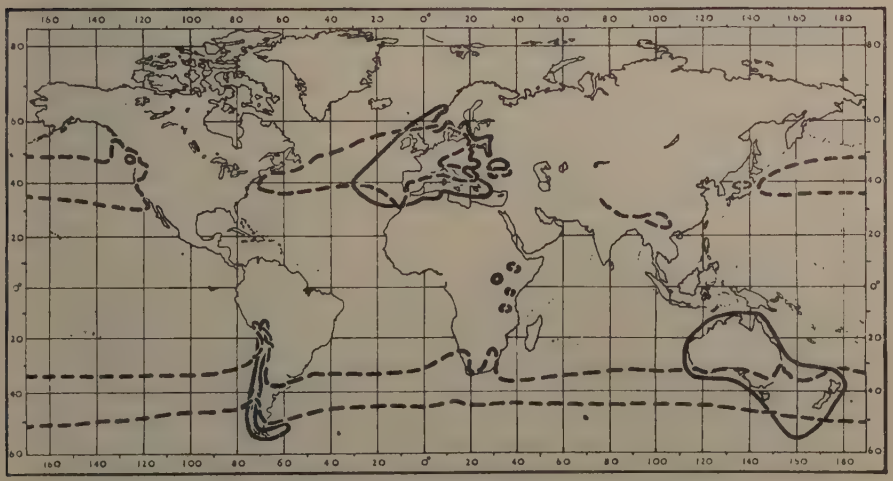
FIG. 20: DISTRIBUTION OF SCHISTOSTEGA OSMUNDACEA AND AREAS BASED ON VALUES OF α AND γ.



——— DISTRIBUTION AFTER GAMS (1928)

– – – AREAS BASED ON α =11° to 43°F. γ = 47° to 72°F.

FIG. 21. DISTRIBUTION OF ORYCTOLAGUS CUNICULUS AND AREAS BASED ON VALUES OF α AND γ.



——— DISTRIBUTION AFTER THOMPSON AND WORDEN (1956)

– – – AREAS BASED ON α = 27° to 61°F. γ = 52° to 74°F.

isotherms is shown for comparison. Fig. 19 shows the area in Eurasia of the common Toad *Bufo bufo* L. after Boulenger (1898). These examples would fit into the same broad pattern.

Areas Related to Centres with Warm Wet Winters

It has been seen in Figs 4–7 that in the latitudes there considered the areas with wet winters and low summer to winter temperature range are found near the west and east coasts of Eurasia and of North America, the most extreme example being centred on the west coast of Europe. The influence of this pattern on biological distributions is often apparent, and a few examples taken from many more which could be adduced will be briefly discussed.

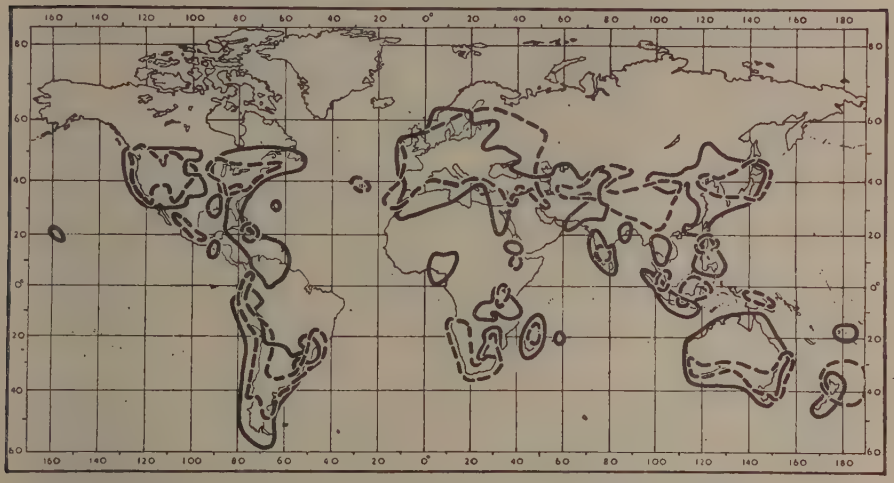
In *Schistostega osmundacea* (Dicks) Mohr., Fig. 20 (after Gams, 1928) an example is seen of a species with a wide distribution in Europe which is also found on the east and west coasts of N. America and to a much smaller extent near the east coast of Eurasia. Boundaries based on suitably chosen January and July temperature limits give a large European area extending to about latitude 47° E. into Russia, and climatically similar zones spreading well inland from the east and west coasts of N. America, while an area is also represented in Japan.

Fig. 21 shows the approximate world distribution of the European Rabbit (*Oryctolagus cuniculus* L.) after Thompson & Worden (1956) and world areas based on appropriate limits of January and July temperatures. It is interesting that the rabbit occurs in the extreme west of South America approximately from latitude 15° S. to the Cape, and at St Juan Island off the west coast of North America, and also in New Zealand and Australia, areas roughly indicated in the map based on temperatures. It does not however apparently occur in South Africa, or in the Asiatic areas which the temperature limits include.

Compared with the areas for *Schistostega*, the European area for the rabbit does not extend so far inland, and both the Japanese area and the east coastal area of N. America have, as it were, been lost into the sea, while the area on the west coast of N. America has become very much smaller.

Fig. 22 (continuous line) shows the world distribution of *Myzus persicae* Sulz. after The Commonwealth Institute of Entomology (1954), and roughly corresponding distributional areas based on January and July temperatures used in the same way as in the above examples, while Fig. 23 is a distribution map based on winter rainfall and latitude. A comparison of these three sets of areas indicates that neither temperatures alone nor winter rainfall and latitude give perfect reproductions of the recorded areas of this insect, but that some correspondence is obtained with either pair of factors. Both sets give a division down the centre of N. America, and give areas of roughly the right size to east and west of this division. Both include virtually the whole of Europe and properly omit the great mass of central and north Asia. Both also include some at least of New Zealand, and both give rather similar Australian areas. In this latter connection reflection will suggest that it is most unlikely that this insect inhabits the desert areas of Australia which its distribution in Fig. 22 has indicated, and in fact the references quoted for this Distribution Map only list South Australia, New South Wales, Queensland, Western Australia, Victoria and Tasmania. That is, North Australia and Central Australia are omitted ; so that the tendencies shown in the areas based on the meteorological factors could be reasonably correct. These two figures also both give some areas in South America and in South Africa, in which places the map based on temperatures seems to be rather better than that based on rainfalls. This present distribution, however, extends beyond the strict terms of reference of the discussion in this paper, since the distribution map shows *Myzus persicae* extending far nearer the equator than the 40° line

FIG. 22. DISTRIBUTION OF MYZUS PERSICAE AND AREAS BASED ON VALUES OF α AND γ.



——— DISTRIBUTION AFTER COMMONWEALTH INSTITUTE OF ENTOMOLOGY (1954).
– – – AREAS BASED ON α = 6° to 72°F. γ = 55° to 77°F.

FIG. 23. DISTRIBUTION OF MYZUS PERSICAE AND AREAS BASED ON VALUES OF ϕ AND ν.

——— DISTRIBUTION AFTER COMMONWEALTH INSTITUTE OF ENTOMOLOGY (1954).
– – – AREAS BASED ON ϕ = 5° to 65° ν = 0·65 to 1·75

of latitude. It should moreover be noted that this insect, in common with many other widely distributed aphids, has two different types of life cycle, one including a sexual generation in autumn with overwintering as resistant ova on a primary host, and one in which the sexual generation is largely or completely abolished ; and it is at present uncertain whether tropical races which live entirely parthenogenetically and viviparously can be regarded as taxonomically identical with the western European form with its full cycle. In regions with a rigorous winter the limiting factor for the species might in some places be the absence of a suitable winter host plant, a factor which might itself be climatically determined. It is however by no means to be supposed that the biological limits described in this and other species are always direct effects of the climatic factors advanced ; very often they must be secondary effects of one sort or another, as for example of competition with other species better adapted to an adjacent temperature range, while often the outcome must be regarded as due rather to a multiplicity of primary and secondary and even further removed factors, nevertheless all affected by the primary climate. Within the scope of the present paper no attempt can be made to trace out all these possibilities for particular species.

Compared with *Schistostega* and *Oryctolagus* the deep penetration south of *Myzus persicae* is coupled with even deeper penetration to the east from Europe, and the areas on the east and west coasts of N. America have become larger, with corresponding area increases elsewhere. Rainfall, as previously seen, has in this case again outlined roughly similar N. American areas to those outlined by temperatures.

Three other examples of plant areas related to this 'warm-wet' complex, for which corresponding areas based on January and July temperatures have been plotted are *Ranunculus lenormandi* F. Schultz, *Picea abies* (L.) Karst. (= *P. excelsa* Link) and *Ilex aquifolium* L., all given by Jeffree (1955 b) ; while an example of a mite having a similar distribution is that of *Acarapis woodi* Rennie given in detail by Jeffree (1955 a, 1957, 1959). *Picea abies* is interesting as representing an example of the possibility already mentioned that a species may be intermediate between those that extend right out to the limits of extremely low temperature range and those that go right out to the limit of extremely high range.

The examples given above are again by no means isolated, for this pattern of coastal Eurasian and North American distributions can be traced in a large number of biological areas. All four coastal areas are seen in *Zostera marina* L. (Ostenfeld, 1927), in *Subularia aquatica* L. (Donat, 1928) and in *Isoetes echinospora* Dur. (incl.: *I. braunii*) (Donat, 1933), while *Veronica alpina* L. (Huber, 1929) is a good example of a west Eurasian and east and west N. American species, the areas being greatest in the two westerly ranges and somewhat less in the east of N. America. Ten species occupying similar east and west Eurasian and east and west N. American areas are given by Hultén (1950) in his Group 9 ('Circumpolar, Arctic-montane plants present in the mountains of Central Europe, but with large gaps in Siberia'), and five more species in Hultén's Group 17 ('Boreal-circumpolar plants that are boreal-montane in Europe but with gaps in Siberia'). In the latter group the reduced size of the east Eurasian areas and the reducing east N. American areas are quite evident. Five more species following the same general pattern are seen in Hultén's Group 21 ('Circumpolar seashore plants'), three in Group 22 ('Circumpolar sub-oceanic plants') and five in Group 33 ('Incompletely boreal-circumpolar plants with a gap in East Siberia'). When Hultén (1937, Plate 15) earlier presented 16 examples of areas showing this same basic distribution as a group of 'Atlantic-Pacific plants' he said, 'Lastly, I would point out that numerous sea animals have distributions that correspond exactly to that of

this group, see, for instance, Hofsten, 1915 (Fig. 8, p. 32; Fig. 15, p. 47; Fig. 17, p. 52, etc.). Their history must be analogous to that of the plants'. Hultén, as already mentioned, was however interested in explaining distribution types on a historical rather than on a climatic basis.

Many other examples may be found of species whose distributions show some of the above features, but do not fill all the possible areas, and the nine examples in Hultén's Plate 38 (1937) could be quoted. It is of course conceded that a great number of species both of plants and insects have not yet colonized every climatically suitable area on the globe, and that this is often the result of some natural barrier to dispersal, such as an ocean. In other instances it could be the result of different competition or other biotic factors. Indeed, it would perhaps be more correct to say that the occurrence of a genus or species in similar climatic areas of two continents is more nearly the exception than the rule. Naturally there are many examples, but at least Cockerell (1932 a; 1932 b) who found discontinuous distribution of some bees (*Hesperapis*) and some plants (*Mendora*) in desert regions of America and of South Africa considered the matter sufficiently interesting on that account to merit a note.

Discussion

It has never been held in doubt (cf. Cain, 1944) that temperature plays an important part in the selection of vegetation types and in limiting plant areas, and in giving some broad tendency towards latitudinally arranged main vegetation zones. In addition it has been recognized (Vahl, 1911; Iversen, 1944) that the temperatures of summer and winter represent the factors operating on plants far better than the annual means. It is not possible to suggest that either the summer or the winter temperature is the more important in deciding a plant's range, since it is clearly known that winter extremes will selectively kill some species and not others, while it is equally known that summer temperatures may also be critical (for example, in the range within which a wheat crop may be obtained)—that is to say, both summer and winter temperatures do really operate upon some plants at some stations. If, however, the findings of Blaauw and his co-workers apply at all widely, it must be supposed that a plant has not only one optimal temperature but a series of optima each (in spring) a little higher than the other and presumably spaced along the time-scale to correspond with the plant's rate of development from one phase to the next. Then the whole annual course of temperature becomes important, and not only the extremes.

The annual course of temperature in these latitudes is roughly sinusoidal, and the annual temperature range coincides with the (double) amplitude of the approximate sine wave of temperature, so that it determines the rate of change of temperatures from winter to summer, and thus no doubt whether the rate of change is suitable for a particular species. The combinations of winter and summer values also approximately determine the number of months during which temperature is in excess of any selected value—for example, above 42° or 43° F. Thus they approximately determine the length of the growing season. These formed the more important of the two factors used by Merriam (1894, 1898) to plot the limits of distribution of animals and plants in N. America.

Most authors have inclined to the view that temperatures in these latitudes are more important than rainfall, and indeed Merriam (1894) had said: 'That humidity is less potent than temperature as a controlling factor in distribution may be shown in several ways ... many genera restricted to particular conditions of temperature range completely across the continent, inhabiting alike the humid and arid subdivisions of their respective zones; but no genus

restricted to particular conditions of humidity ranges north and south across the several temperature zones.

'Humidity and other secondary causes determine the presence or absence of particular species in particular localities *within* their appropriate zones, but temperature predetermines the possibilities of distribution ; it fixes the limits beyond which species cannot pass ; it defines broad transcontinental belts within which certain forms may thrive if other conditions permit, but outside of which they cannot exist, be the conditions never so favourable'.

It would nevertheless be wrong to assert that temperature is all-important, and it must be remembered that the considerable correlation which has already been shown between rainfall and temperatures might make it possible for effects on the plants properly attributable to rainfall to appear to be results of temperature levels. It should also be recalled that Hooker (1922) and Geddes (1922) obtained similar levels of (partial) correlation coefficients with rainfall and with temperature for crop yields, which as aspects of plant responses may not be unrelated to plant distributions. Indeed, the comparatively recent discovery of the very considerable effects of day-length as a new factor affecting plant growth could serve as a warning against the formulation of final conclusions at this stage as to the extent to which temperatures, precipitation limits or day-lengths might be determinative. Both Köppen and Thornthwaite used temperatures as the main factors in their systems for plotting vegetation types, but both found it necessary to use rainfall factors as well—though indeed the necessity for introducing rainfall was apparently much more urgent in tropical than in temperate latitudes. As has already been suggested, the work of these authors does not prove that day-length (or latitude) considerations are unnecessary, since they have in effect been approximately introduced in the temperature criteria adopted.

Limiting the discussion, however, to very broad patterns of climatic differentiation across the continents at the latitudes which have been considered above, it is clear (1) that there is an area in eastern Siberia colder and with drier winters than anywhere else, (2) that at the other extreme there is a western European area which has a combination of lower annual temperature range combined with higher winter rainfall than almost any other place (except for small corresponding areas on the west coast of N. America), and (3) that there is a sequence of zones, not exactly, but broadly defined, with temperature specifications and at the same time very approximately corresponding winter rainfall specifications. It is however understood that since the correlation between winter rainfall and annual temperature range is only about 0·6 there would equally be transitional and other areas where there were major departures from these relationships between the two sets of factors.

If winter rainfalls at given latitudes were operative factors in the selection of plant areas it would still be expected that a pattern recognizably similar to that obtained from a selection based on January and July temperatures would follow ; and if it should be the case that these two sets of factors (summer and winter temperatures ; latitudes and winter rainfalls) operated together in a joint selection there would again be strong reasons for expecting that plant areas would show some of the broader elements of plan which have been seen in Figs 4–7.

It may be wondered why winter rather than summer precipitations have been used in the above treatment, for it might be supposed that the latter would be the more important to the plant. The meteorological reason why winter rainfall makes a selection akin to that made by winter temperature is that there is a powerful interplay between these two physical elements. It has already been seen that moist air, because it is less often clear, reduces the heat losses from the land in winter, and so protects the area from excessively

low winter temperatures, and that this is found particularly near the coasts. There is, however, a reciprocal relationship, that a large expanse of very cold land cools the air, and that such very cold air over a large land mass in winter cannot carry, for reason of its temperature, more than a very little water. Thus in winter it becomes very difficult indeed in these latitudes for any large amounts of water to reach the centres of very large land masses—that is to say, the coldest areas inevitably tend to have the lowest winter rainfalls.

In the summer the picture is very different. The land masses are everywhere warmer, and indeed tend to heat up in the centre more quickly than at the coasts, and the air travelling over the land is able to carry some of its moisture far inland. The coastal and inland rainfalls vary much less, though the coastal rainfalls still tend to be somewhat higher in general than those inland. The main winter rainfall pattern therefore gives a much better indication of the fluctuations in the mean annual pattern of rainfall than does the summer rainfall.

Just as the winter isotherms across Eurasia show great inclination relative to lines of latitude, and great extremes, and the summer isotherms much more nearly approach lines of latitude, the winter isohyets also show much greater extremes and inclination than those for the summer months (Figs 1 and 2). From the nature of their course the summer isohyets could not therefore apparently make any so dramatic separation of climatic types in an east-to-west direction. Only near the coasts do they show great inclination to lines of latitude, and here they increase in the same sort of way as do the winter isohyets.

Cain has been quoted as pointing out that plant geographers have for a long time recognized the broad parallel between temperature belts and vegetation, and the subdivision of these belts on a moisture basis. Such temperature belts are usually taken in this broad sense to mean either bands of mean temperature, or of summer temperature—that is, they are belts which broadly correspond with latitude ranges, though in detail they define the plant-geographical areas rather better than do strict bands of latitude (cf. Brooks, 1956, who refers to Supan's use of such bands for the above reasons). It has been seen above that, within the 40°–70° latitude band, winter rainfalls will subdivide such bands rather well, and that if annual rainfall is used the subdivisions will result, in the main, from the winter rather than from the summer components. It is also clear, however, from the above discussion, that in the broad sense in which Cain was speaking, summer temperature belts subdivided on a basis of winter temperature make the same essential type of separation as such belts subdivided on a basis of winter rainfall (or indeed subdivided on a basis of annual rainfall).

The separations of climatic zones shown in Figs 4–7, subdivided by January and July temperatures and by latitudes and winter rainfalls, can in fact be given alternatively, in so far as the same essential broad patterns are concerned, as July temperature bands subdivided by winter rainfall, and also as latitude bands subdivided by January temperatures.

While they have not discussed the subject in the above terms, it is therefore seen that these are the same types of broad climatic division which geographers have 'long recognized' (Cain) as giving subdivisions of vegetation types. If they separate vegetation types it could have been expected that they would also have contributed to the separation of specific plant areas.

No attempt has been made, nor indeed did it seem possible, to assess statistically the degree of fit obtained in the above examples, but it can now be suggested that while earlier papers had indicated that these temperatures are appreciable influences in plant distribution, this method of plotting whole areas can be taken as indicative of the approximate manner in which the operative importance of temperatures in their influence on limits of plant

distributions must be supposed to act. The different parts of the circumferences of the ellipses on Cartesian co-ordinates (cf. *P*, Fig. 3) can be shown to correspond with different parts of the perimeter of the plant area on the geographical map, and therefore in so far as temperatures are operative, it is seen evidently to be true that two summer temperature limits, an upper and a lower, govern different parts of the perimeter of the plant area, and two winter temperature limits approximately govern other particular parts. The influence of these four factors must indeed be supposed gradually to pass over from that of the coldest January (or winter) limit to the warmest July limit, then to the warmest January limit, to the coldest July limit and finally back to the coldest January limit (which may better be appreciated from an examination of the areas in Fig. 3). This would be one main reason why the fitting of isotherms to area boundaries has not been generally successful in the past—the fit may be very good over the region where one extreme limit of January or of July temperature is operating alone, but further round the area perimeter the influence of this one factor will be diminishing and that of another temperature limit will be taking over, and a departure of the plant distribution limit from the single isotherm line must necessarily follow.

The criticism may properly be advanced that, as indicated earlier, these are not the only factors determining plant areas. That is true, but it does not alter the indication that in so far as temperatures play a part their operation must be broadly in the manner stated.

Hultén considers the geographical distributions of plants from the point of view of their assumed dispersal from a centre or centres. He considers what might happen if 'a number of different plants were placed within a large area of suitable soil cleared from all vegetation and allowed to develop under equable and favourable conditions without competition from other plants. Each species would spread in all directions around the original centre, but it could hardly be expected that all plants would spread with the same rapidity. . . . The result would doubtless be approximately circular areas of different size around the centre'. . . . 'In nature the areas doubtless rarely attain the theoretically circular form. . . . There still remains, however, the chief feature of comparatively recent areas, their concentricity around the place from where they radiated'.

Such a theory is based on climates of the past, and no critic can expect that these should be stated with detailed exactitude, although it does seem to the present writer strange that the centre of the EPAs at present under discussion has a January mean temperature of −27° F. (that is, averages 59° F. of frost), and is not far south of the coldest spot in Siberia and in the whole of Eurasia. The coldness of this area has already been seen to be the result of its position within the largest of the land masses, and is partly the result of a wind direction brought about by the direction of revolution of the earth, and it would apparently require a reversal amounting to complete alteration of sizes and positions of land and sea masses for it ever to have been one of the warmest places in Eurasia, in which alone such plants were able to survive.

It has however been seen that almost exactly similar progressive areas can be obtained by invoking the known temperatures of today rather than making assumptions about those of the past, and that a series of species having progressively wider temperature tolerances will on the basis of the present handling show 'equiformal progressive areas' in the direction of the plant areas.

No claim is implied that all biological areas can be reproduced to such a considerable extent on a basis of present-day factors, or by the methods which have here been adopted. It is admitted that there are bound to be considerable if not sometimes major discrepancies in areas based on the factors here used, while it is equally appreciated that there are some kinds of habitat (particularly

mountain areas and perhaps sea coasts) for which the meteorological data at present used are entirely inadequate, so that it could not be expected that montane species should in general be able to have their areas easily matched by areas obtained in the present way. There are also errors in the presentation of plant areas themselves, by whatever author, and errors in the meteorological data. There is also no doubt a great deal of truth in many of Hultén's suppositions, but it is suggested that the picture could well be amplified by a consideration of present-day climatic factors. These can hardly be handled, on a scale corresponding with that of Hultén's work except by a technique such as has been adopted above.

The climatic patterns which have been discussed are well established, and in so far as temperatures, rainfalls, and day-lengths affect areas it seems unlikely that they should operate otherwise than broadly in terms of the general plan which has been presented, or of relatively minor modifications of that plan. Modifications which seem probable are in the exact shape and orientation of the figure, on Cartesian co-ordinates, for which an ellipse has been used. The author has indeed already collected evidence that the axis of that figure, when temperature co-ordinates are used, is not exactly parallel with the January temperature axis, but is generally inclined to that axis. This will be considered in a subsequent paper. It is again possible that parameters slightly different from those here selected may prove appreciably better —for example mean annual maximum and mean annual minimum temperatures might theoretically be better in some respects that July and January means, though the author, using the maps of Brooks & Thorman (1928) has not been able to show any improved fit.

While the present work is not in a form to give any definite evidence on the relative importances of the several factors used, the general tenor of the results suggests that probably temperatures are generally the dominant factors in the biological distributions here discussed, as had earlier been supposed. Prior to this treatment, however, it might have seemed highly presumptuous to attempt to define biological areas in terms of temperatures alone since rainfall and day-lengths are known to have considerable effects. But it now appears a little less unreasonable, as an interim measure of practical expediency, to try to work out areas in this way in these latitudes, since the selections based on the temperatures tend usually to give reasonably appropriate selections of rainfall and of day-lengths also. Thus if temperature is in fact the dominant factor and the others of appreciably less importance it may not often be the case that they are in sufficient opposition in the areas selected on the temperature basis to cause major discrepancies. It is obvious, however, that eventually the relative parts played by temperatures, rainfall and day-lengths must be determined in a wide range of different biological distributions.

There have hitherto been a number of attempts (Merriam, 1894 ; Vahl, 1911 ; Köppen, 1918 ; Thornthwaite, 1931, 1933 ; Hopkins, 1938) to determine the boundaries of vegetation types on a climatic basis. None of these have been perfect, but they have nevertheless been interesting and useful for some, purposes. This paper now presents a method of plotting approximations to the areas of particular species, and the advance claimed is that of bringing the subject forward from the stage of a relatively general definition of the climates of broad types to the particular definition of climatic factors related to the areas of species. As in the case of the earlier authors the results are not exact and the treatment therefore not final, but while it still does not allow biological areas to be determined exactly, it is hoped that it may give a further key to the understanding of them and some probable reasons for their limitations in particular directions.

Acknowledgments

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Summary

Temperature, rainfall and day-length probably all help to determine limits of plant distributions, but the distributions cannot generally be explained by simple values of any of these quantities alone. There is in most latitudes a negative correlation between annual temperature range and log. winter rainfall and this and other correlations make it difficult to distinguish the effects of the several factors in the delimitation of plant areas.

Approximately within the 40°-70° N. latitude band a strongly marked climatic pattern of increasing annual temperature range inland from the coasts is matched by a pattern of reducing winter temperatures in the same directions. The centre of this pattern, in Eurasia, is in eastern Siberia. This pattern is reflected in many plant areas. Following ideas expressed severally by Vahl, Iversen and Jeffree for plotting plant distribution in terms of temperatures of coldest and warmest months (or of January and July) on Cartesian co-ordinates it is shown that the areas obtained may be closely related to the above main climatic pattern. Very similar areas may be obtained from values of latitude (which governs day-length) and log. winter rainfall.

Several of these climatic areas have been compared with biological distributions and maps are presented. Some of these can be arranged in progressive series which correspond rather closely with some series of equiformal progressive areas of plant distributions given Hultén.

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SYMPOSIUM

EXPERIMENTAL TAXONOMY OF VASCULAR PLANTS

LINNEAN SOCIETY, 6 MARCH, 1959

INTRODUCTORY REMARKS

By PROFESSOR D. H. VALENTINE, F.L.S.

PERHAPS the most useful contribution which I can make in this short introduction is to define experimental taxonomy. In my view it can be regarded as the study of evolutionary processes in plants and of the bearings of this study on their taxonomy. I think that the papers to be presented here today will illustrate this definition, though as is natural, one paper will tend to emphasize the evolutionary side of the subject, and another, the taxonomic side.

The scope of the investigation undertaken by the experimental taxonomist may also vary considerably. Thus one investigator may concern himself merely with a local population, another with a species complex or a genus, and yet another with a family or even a phylum. This point too will, I think, be well illustrated by the papers which are to be read today.

I need say no more except to express a wish that the discussion will be as free and as lively as possible.

RECOGNIZING ADAPTIVE VARIANTS

By D. A. WILKINS

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THE idea of adaptation has been discussed in many different contexts, but its experimental study has quite a short history. When Turesson described the first ecotypes he regarded the morphological characters by which they were distinguished as adaptive, but even at that stage he recognized that adaptation was a much more subtle business than the mere association of a particular morphological type with a particular habitat. He pointed out that the adaptedness of an individual depended on its whole genetic constitution, and implied that physiological differences were likely to be much more important to a plant's survival than morphological ones. This fact has been rather neglected in some later discussions, perhaps because morphological characters are both easier to study and of first importance to the taxonomist. This neglect may be justified in the case of really big taxonomic differences between species and genera, where it is sometimes possible to pick on single conspicuous characters whose adaptive significance can hardly be doubted. This seems particularly true in animals. Many specialized features in the morphology of mammalian species, for instance, can be related to unusual modes of life. When we are dealing with the small differences found within species, on the other hand, and especially in plant species, their adaptive value is rarely obvious and it is easy to make unjustified assumptions about their selection in the wild.

When designing experiments to investigate small differences it is essential to think in comparative terms. In a sense any plant which survives and reproduces is adapted to its habitat, and the discussion only becomes meaningful when we try to show that one type is better adapted than another to a chosen

habitat. I do not feel that the converse type of experiment, in which one type is tried out in a number of habitats, is so easy to interpret. If the same type is put into several wild habitats with a view to finding which one suits it best some measure of fitness has to be found for comparison. Even if this can be done satisfactorily we are likely to find that the best habitat in the absence of competiton is no longer the best when other species are present. The experiment in which two types are allowed to compete in the same habitat is much easier to analyze because measurements of fitness need not be used at all. The type which spreads at the expense of the other is the better adapted, by definition. There still remains the difficulty of extrapolation. Other people are not likely to be interested in our particular test habitat, and some way must be found of defining the ecological limits within which our results apply. This entails the replication of the experiment in a number of sites of similar apparent ecology. If concordant results are obtained we have some idea then of the generality of our conclusions. Even this may not be as simple as it looks, because we have to use some kind of descriptive ecological classification, which will identify the group of similar communities within which one of our types is superior to the other. Replication in space may not be sufficient. If the same competitive experiment were repeated in a number of years in the same plots of ground there is no reason to expect the results to be always the same—one type might survive best in a dry season and the other in a wet one.

You will gather from this that I feel that the direct comparison of individuals under wild conditions is liable to produce results which are difficult to interpret, and the use of controlled conditions might be considered instead. The difficulties then are certainly different, but they seem just as serious. It is easy to replicate the experiments many times under the same conditions, and to alter the conditions in a planned manner if desired, but in spite of these advantages there remains the final step of extrapolation to the wild, which is surely in most cases extremely speculative. With any imaginable equipment controlled conditions differ greatly from wild ones, and I cannot see that a controlled environment chamber is of great use for the solution of the ordinary problems of comparative adaptation in the wild. I shall be discussing later a particular situation which was sufficiently abnormal for this method to be of some use, but first we must briefly examine the alternatives to direct competition and see what can be done with other types of experiment.

Any other kind of evidence for superior fitness is bound to be circumstantial, but a good deal can be learnt from it all the same. If a species is sampled over a range of habitats within a small geographical area and the samples grown in a suitable layout in the experimental garden, any significant differences found between plants from the various habitat types may be assumed to reflect differences of genetic constitution. If certain precautions both in sampling and in statistical analysis are observed it is possible to say with some confidence that such genetic differences are of an adaptive nature, since the only way to account for their existence is by natural selection. In a slightly more elaborate case it is possible to get an actual numerical correlation between the variation in a plant character and that in a measured habitat factor, and again in suitable circumstances this may be interpreted as the result of adaptation and selection.

These methods of comparative cultivation are valuable, and in many cases are the only ones available, but they suffer from a slight uncertainty about what is being measured. The important character may not be the one measured in the trial but another closely related to it. In particular the measured character may be merely one morphological expression of a profound physiological difference. Similarly the plant may be responding not to the measured habitat factor but to one correlated with it. As an example we have soil acidity, which it is now realized may sometimes be important in itself but which is much more

often important because it acts as an approximate indicator of the availability of other ions. This makes it impossible to assume that a correlation between, for example, leaf size and soil acidity represents a directly adaptive relationship.

The other difficulty about demonstrating natural selection in the wild is that it may often be of low intensity. Two plants may be in fact adapted to different habitats, but if the differences are slight the fact may be extremely difficult to demonstrate. When I started work on this problem I was much attracted by the case of industrial melanism in moths, and I decided to look for a case in plants where selection was so intense that only one type could survive, so that I should not have to deal with a delicate competitive balance which could be easily tipped one way or the other. It was also desirable to find a habitat factor which could be relied upon to remain constant during the experiments and which was reasonably easy to measure.

Thanks to a suggestion by Bradshaw (1952) I found such a situation on the waste tips from old lead mines. Here was a poisonous soil on which few plants would grow, and whose properties were likely to remain the same for years on end. There is still much work to be done on the comparative ecology of those species which do grow on the tips, especially as they vary from one locality to another. The one species which seems to be universal is *Festuca ovina*, and that was chosen for detailed investigation, but in South West Scotland it is associated with *Deschampsia flexuosa*, in parts of Wales it is subordinate to *Agrostis tenuis*, and in the limestone districts of the north Pennines it is accompanied by *Minuartia verna*.

A preliminary experiment on the soil samples collected at the same time as the *Fescue* showed that it was poisonous to normal plants of that species. Fortunately, the obvious guess as to the nature of the poison turned out to be the right one. The soils contained very large amounts of lead, and it was satisfactory to find that plants from the tips could continue to grow in a culture solution containing enough lead nitrate to stop the growth of ordinary plants. This was made the basis for a method of measuring the lead tolerance of each individual plant. Tillers were put in narrow glass tubes and allowed to root, and the rates of root growth in culture solutions with and without lead were compared. When the resulting tolerance indices of the individual plants were examined they were found to form a continuous series from one extreme to the other, but the population means were not scattered over the whole range but clustered around three values. Instead of just tolerant and non-tolerant plants I seemed to have a medium tolerant grade as well. Unfortunately, the method has not so far proved accurate enough to measure the tolerance of an individual plant. This would have settled the matter, but the only explanation I can see for the grouping of the population means is that there are three types of plant and each population consists almost entirely of one kind. The definite proof of this discontinuity is one of the crucial points still outstanding.

Summing up the general picture of the distribution of tolerance in the wild material: the species was divided into probably three types—the normal one which would not root in my test solution of lead nitrate, a medium tolerant one which would only root slowly, and a highly tolerant one whose roots seemed little affected. The character of tolerance was rigidly associated with a particular soil type, the tolerant plants coming from soils containing up to 4 per cent lead and all the non-tolerant ones from soils containing very little. There seemed little doubt that the selective factor had been correctly identified, and that the results obtained under controlled conditions could be used with confidence to explain the observed wild distributions. Differential rates of root growth, with complete stoppage at one extreme, could surely be regarded as directly adaptive characters on which the presence of lead in the soil would

exert a strong selective effect. Non-tolerant plants were completely unadapted to growth on the tips.

The next point of importance was the genetic nature of this adaptive difference. Plants showing the three degrees of tolerance were crossed in all possible combinations, and as soon as the progenies came to be tested it was clear that tolerance was completely dominant. Again the lack of precision in testing made it impossible to analyze the results any further, as the individuals of the progeny could not be classified with certainty into their proper tolerance groups, and so genetic ratios could not be calculated. In the backcrosses there are clear signs of segregation, but the actual number of genes is still in doubt—it may be only a single pair of alleles.

The prospects of finding a simple genetic system behind the varying tolerance improved considerably when a tolerant diploid was found. The plants from Leadhills, which I visited first, were all tetraploid, but in the Pennines the two races are thoroughly mixed up and in one or two cases I found tolerant plants of both races on the same tip. It was interesting to find that the degree of tolerance seemed to be much the same in the two races. It may even be possible to decide whether or not it is the same gene in both cases, as on one tip the triploid turned up together with both its presumed parents. It will be interesting to see if it can be backcrossed to either of them. My first impression was that the transfer of the gene from one race to the other was extremely unlikely, but if the triploid turns out to be less rare and less sterile than expected this may have to be revised.

The plants I have been describing all have in common the ability to grow in the presence of large amounts of lead. This results in their being able to colonize a habitat from which other plants of the species are excluded, and it might be tempting to regard them as a distinct entity which could be described as an ecotype. If, however, their distinctive growing ability could be treated as a single character, due perhaps to a single major gene, it would surely be misleading to separate them in this way, and so a garden trial of the Scottish material was laid out to try and find other characters which might be associated with tolerance and which could be used to recognize the race in the herbarium. The short answer is that none were found. Regional differences were found in many morphological characters, and similar differences between populations, but the lead tolerant plants as a whole seemed to have no morphological characters in common by which they could be distinguished from non-tolerant ones. Apart from that rather negative conclusion this trial provided a new and completely unexpected piece of information. *F. ovina* is usually easy to grow in the garden, and apart from the ordinary hazards of cultivation it is quite normal for virtually all the plants in a trial to flourish. A large number of plants in this trial did not flourish—they were looking weak by the end of the first summer and by the spring many had died. The significant fact was that the dead ones were almost all lead-tolerant. I still do not know why this happened. The possibilities are obvious—lead tolerance was associated with another character which weakened the tolerant plants in ordinary soil. That other character might be a susceptibility to some other normally innocuous substance in the soil, or a requirement for something available on the tips but not in the garden—possibly even for lead itself. This may explain why I have never found a tolerant plant away from a lead tip.

If there is some good reason why tolerant plants are confined to poisonous soil this also has a bearing on their mode of origin. Suitable habitats are rare and very scattered—Leadhills is separated by nearly a hundred miles from the nearest mines in the Pennines, and there are further gaps between there and the Lake District and Wales. With a dominant gene of this kind there is no chance of concealed spread through the intervening populations and it could only get

from one area to the other by the direct transfer of pollen. Even with a wind-pollinated species it seems to me more likely that the gene arose by mutation separately in the various areas. If that is so, it will be interesting to see whether it is always the same gene, or whether a number of loci produce mutants with similar properties.

Whatever the detailed genetical picture turns out to be it seems to me most dangerous to describe the tolerant form in terms which might suggest it was a homogeneous race, or even perhaps a minor taxonomic unit, and for this reason I have avoided the term ecotype. It is true that the ecotype is an experimental rather than a taxonomic category, and ecotypes must not always be expected to be morphologically distinct, but surely it is more misleading than helpful to describe a variant caused by a single major gene as an ecotype. Even at that low level I feel we ought to apply the taxonomic principle of insisting on a correlated set of characters, rather than a single diagnostic one, however important in the life of the plant that one may be.

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LUZULA CAMPESTRIS (L.) DC.[1]

By Janet Buchanan

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Luzula campestris (L.) DC. is a species whose taxonomic content has varied considerably. According to Buchenau's *Monograph of the Juncaceae* (1906) the species is divided into 20 varieties, which occur mostly in the north temperate zone and in Australasia. Only four of these varieties occur in Britain: *pallescens* Wahl., *vulgaris* Gaud. (*campestris* s.s.), *multiflora* Čelakovsky and *congesta* (Thuill.) Buchenau. They are treated in *The Flora of the British Isles* (Clapham, Tutin & Warburg, 1952) as three species, with *congesta* as a variety of *multiflora*. *Pallescens* is very rare, growing only in the Fenland, while the other three taxa are common and widespread. *Campestris* is found in dry pastures, *multiflora* usually in moist woods and *congesta* usually in more open moors and bogs. Because of its rarity in Britain, and because mass gatherings would have been required, *pallescens* was omitted from the investigations summarized in this paper.

Populations of *campestris* found in the field are usually reasonably pure, but *multiflora* and *congesta* often grow together; a population of either frequently has at least a few plants of the other growing with it.

Morphologically, *campestris* is separated from the other taxa in having shorter stems and leaves, longer stamens whose anthers are twice as long as the filaments, and more or less spherical seeds. Of the two taller taxa, *multiflora* has smaller seeds and flowers than *congesta*, as well as having a lax inflorescence instead of a congested one.

Collections were made where the habitats of two taxa met and overlapped, where hybridization, if it could take place (as was suspected), would be most likely to occur. Other gatherings were made from relatively pure populations of the taxa; samples of at least 25 plants were taken from 50 populations.

[1] This paper represents a summary of a paper read in the Symposium held on 6 March 1959, entitled, 'A re-examination of *Luzula campestris* s.l.'—(Ed. Sec.)

In one locality, in Glen Lyon, the area to be sampled was divided into five zones, parallel to the junction of the two types of habitat into which it could be divided. These habitats were pasture, containing *campestris*, and, at a lower level, a bog containing *congesta* ; between them was a grassy slope on which grew both *congesta* and *campestris*, along with a few plants of *multiflora*. About 25 plants were collected from each zone.

A scatter diagram of leaf length and stem height of all these plants showed a continuous variation in both characters. On the other hand, a scatter diagram of seed and stamen characters shows two separate groups of plants, one being *campestris* and the other *multiflora* and *congesta*. This suggests that the environment modifies vegetative characters to give intermediate forms, but that floral characters remain distinct, indicating the absence of hybridization in this instance, even though the habitat might have permitted it.

In the case of *multiflora* and *congesta*, the vegetative characters in the field show no significant difference, and the most obvious character separating them is the degree of congestion of the inflorescence, that of *multiflora* having four to ten heads, each on a fairly long stalk, while *congesta* has more or less sessile heads. This feature is correlated with the size of the seeds and the length of the perianth segments. The division into two groups is less distinct than it is when these two taxa are compared with *campestris*.

In order to compare all three at the same time, a modification of the ' Hybrid Index ' (Anderson, 1949) was used, which was essentially the same as the first stage of the calculation of a discriminant function (Whitehead, 1954). Two indices, based on the floral characters distinguishing the taxa, were calculated, to separate (*a*) *campestris* from *multiflora* and *congesta* (*X* index) and (*b*) *congesta* from *multiflora* (*Y* index). The actual value for each character was converted to the corresponding value on the scale 0–50, and the sum of these numbers was the index value for each individual plant. The value of *X* for *campestris* is low, while for *multiflora* and *congesta* it is high ; in the case of the *Y* index, the values for *congesta* are high, and *multiflora* falls in the lower part of the range. The total ranges of variation of the indices are, approximately : *X*, 40–150 ; *Y*, 30–130. The *X* and *Y* indices of individual plants can be plotted on a scatter diagram ; a large sample of over 1000 plants from widely separated localities was used. The dots representing these plants showed three areas of concentration, each of which was equivalent to one of the taxa. The *multiflora* and *congesta* groups are less clearly separated from each other than they are from *campestris*.

This type of morphological relationship was again observed when 12 gatherings, of five or six plants each, were grown under cultivated conditions. There were three gatherings each of *campestris*, *multiflora* and *congesta*, and three in which *congesta* and *multiflora* were mixed. Three groups were again apparent when *X* and *Y* were worked out and plotted against each other.

As Nordenskiold (1951, 1956) has shown, the *campestris* group of the genus *Luzula* forms a polyploid complex ; the chromosome numbers of the cultivated plants were therefore determined, successful counts being obtained for about half of them. The results corresponded with those of Nordenskiold, although no tetraploid *multiflora* or hexaploid *congesta* were found. When this information was superimposed on the scatter diagram of *X* and *Y*, it was found that all the diploids ($2n = 12$) were in the *campestris* group, all the hexaploids ($2n = 36$) in the *multiflora* group and all the octoploids ($2n = 48$) in the *congesta* group. Five plants with $2n = 42$ were found ; in the diagram three of them fell in a position intermediate between *congesta* and *multiflora*, one was in the *congesta* group, and one was in the *multiflora* group. These plants were all from the mixed gatherings, which included three or four wholly or partially sterile plants, and also several which had one or two stalked heads in an otherwise

congested inflorescence. It seems most probable that these plants are natural hybrids between *multiflora* and *congesta*. No hybrids between *campestris* and the other taxa were found.

These results clearly support the retention of *Luzula campestris* as a separate species. The differences in morphology and chromosome number, and also in ecological and geographical distribution, seem to me to be sufficient to justify the consideration of *congesta* as more than a variety, or even a subspecies, of *multiflora*. Specific rank is therefore recommended for both *Luzula multiflora* (Retz.) Lej. and *L. congesta* (Thuill.) Lej.

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THE EXPERIMENTAL TAXONOMY OF EUROPEAN *CALLITRICHE*

By J. P. Savidge

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The eight species of *Callitriche* occurring in Europe can be grouped into two distinct sections of the genus : *Pseudocallitriche* and *Eucallitriche*. The *Pseudocallitriche* have flowers without bracts, linear leaves without stomata or pellucid glands, a basic chromosome number of $x = 3$ and are always completely submerged : the *Eucallitriche* have two bracts to each flower, linear to ovate leaves with stomata and pellucid glands, a basic chromosome number of $x = 5$ and can be either submerged or terrestrial. The two European *Pseudocallitriche* species, *C. hermaphroditica* L. (*C. autumnalis* L.) and *C. truncata* Guss. show little morphological variation but the six *Eucallitriche* species are extremely polymorphic and occur in a wider range of habitats.

An important aspect in the study of the polymorphic species, belonging to the *Eucallitriche*, is the investigation of characters used in the separation of the species. This has been done in two ways : (i) by making a biometric analysis of populations of the same species growing in widely different habitats, and (ii) by placing clonal sub-cultures into different habitats. Although the results of this investigation are not yet complete the data so far obtained indicate that certain characters such as leaf-shape are phenotypically extremely variable ; stamen and stigma length show some variation in size but they can be used for the separation of species providing an allowance is made for differing environmental condition ; other characters such as mericarp size, width of mericarp wing and pollen diameter show little variation.

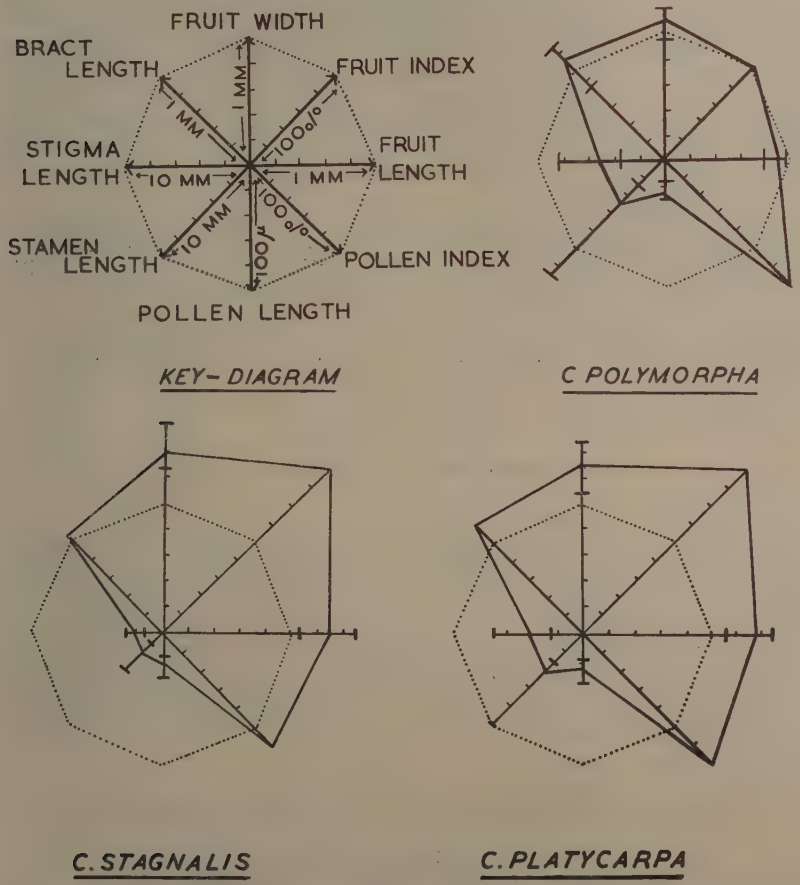
If an accurate separation of the species is required a microscope should be used for measurements of characters such as length of stamens and mericarp and width of mericarp wing. After identifying plants from a large number of populations experience is gained of other characters such as colour and texture which provide additional guides to the separation of the species

Probably the most effective means of identification is by comparing the population under investigation with a series of species polygons. The polygons used in the figure are based on 300 measurements for each character and are

obtained from plants growing in all the habitats in which the species are found.

Controlled interspecific hybridizations to determine whether it is possible to produce hybrids have been carried out. In inter-specific cross pollinations using 5,000 flowers from 140 cultures there was only one cross in which viable fruits developed. The mericarps of this cross, between *C. platycarpa* Kütz.and *C. stagnalis* Scop., took a month to germinate (three to five days is the normal germination period), grew slowly and after the development of the third pair of leaves the seedlings turned yellow and died.

Observations at localities in which three or four species of the section *Eucallitriche* grew intermingled did not reveal any plants of apparent hybrid origin, even after all four species had been flowering at the same time. Only one naturally occurring hybrid population of *Callitriche* has been found during



Polygons of *C. platycarpa*, *C. polymorpha*, *C. stagnalis* and key-diagram. Note the intermediate position of *C. platycarpa* between the other two species. The thick continuous line linking the radii indicates the mean value for each character or character index. The extreme limits for each character are indicated by transverse lines across the relevant radii. The dotted lines and calibration markers on the radii are measuring guides. Fruit index is 100 length × width ; pollen index is 100 length/width.

the last five years. This hybrid population was at Hillerød, some 35 km. north-west of København. Construction of a polygon indicated that it was intermediate between *C. platycarpa* and *C. polymorpha* Lönnr. and examination of first meiotic metaphase in pollen mother cells showed that it was a triploid with one quadrivalent, three bivalents and five univalents. Such pairing indicates that there was a probable ancestral relationship between the diploid and tetraploid parents of the hybrid. From a study of this hybrid population (to be presented in another paper) there is good evidence that *C. platycarpa* (2n = 20) is an allotetraploid derived from *C. polymorpha* (2n = 10) and *C. stagnalis* (2n = 10). The figure shows the intermediate position of *C. platycarpa* between the two probable parental species.

It is the presence of the three closely related species, *C. platycarpa*, *C. stagnalis* and *C. polymorpha*, in North-west Europe that has caused botanists so much difficulty over the last 130 years. Biometric studies have shown the three species to be distinct and the artificial hybridizations have indicated that *C. platycarpa* and *C. stagnalis* do not readily interbreed. The past difficulties have been mainly due to botanists failing to recognize *C. platycarpa* as a distinct species. At the best *C. platycarpa* has been given varietal rank by British botanists and a number of Continental botanists have regarded *C. platycarpa* as a synonym of *C. stagnalis*.

In Britain it has been found that *C. platycarpa* is a common lowland species but that it is extremely unlikely that *C. polymorpha* and *C. palustris* L. (*C. verna* L.), which have normally been included in British floras, occur in the British Isles. They are, however, common throughout Fennoscandia.

ASPLENIUM TRICHOMANES: A PROBLM IN THE TAXONOMY OF POLYPLOIDS.

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SUMMARY

Asplenium trichomanes is an aggregate species within which are included three different cytotypes corresponding to diploid, tetraploid and hexaploid levels of polyploidy. Cytogenetic analysis of a series of artificial hybrids has demonstrated the close genetic inter-relationship of the entire species complex although hybrids formed between plants of the different cytotypes are infertile. Taxonomic description of the three cytotypes is difficult since they can be discriminated only on a basis of ' micro-characters '. The possible taxonomic treatment of the constituent parts of this species aggregate was discussed.

EVOLUTION WITHIN THE GENUS DRYOPTERIS

By S. WALKER

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MANY representatives of the genus *Dryopteris* in Europe have evolved as a result of the processes of hybridization and polyploidy. Evidence for this was shown by Manton (1950) and S. Walker (1955) from which the following examples may be cited.

D. abbreviata (Lam. & DC.) Newman is diploid (the basic chromosome number in *Dryopteris* is $x = 41$) and part parental to the tetraploid *D. filix-mas* (L.) Schött. *D. borreri* Newman reproduces apomictically and exists in both diploid and triploid forms. These forms hybridize with sexual *D. filix-mas* in the wild to give rise to apomictic tetraploid and pentaploid individuals. *D. villarsii* Woynar is represented by diploid and tetraploid forms. The *D. spinulosa* complex includes three allotetraploid species, *D. cristata* (L.) Gray, *D. spinulosa* (O. F. Müll.) Watt and *D. dilatata* (Hoffm.) Gray, requiring at least four ancestral diploids to account for their origin. One of these ancestral genomes, that which is part parental to both *D. spinulosa* and *D. dilatata*, is now represented by two distinct diploid forms of '*D. dilatata*'; one is found in Britain and on the continent of Europe, the other in the island of Madeira. The latter form has been named *D. maderensis* (Milde) Alston (1956). Hybrids between members of the complex occur on triploid and tetraploid levels.

An investigation of material from N. America has shown that the *D. spinulosa* complex is well represented and closely parallels that in Europe. *D. cristata* and *D. spinulosa* are present in most northern States ranging across the continent and are tetraploid. So-called '*D. dilatata*' occurs in the NW. States but is diploid and a further diploid, *D. intermedia* (Muhl.) Gray, exists in the NE. States. Experimental hybridization indicates that the diploids '*D. dilatata*' from NW. States, from Britain and Europe, from Madeira and *D. intermadia* from the NE. States all represent the same ancestral genome (S. Walker, unpublished). *D. intermedia* readily hybridizes with *D. spinulosa* and *D. cristata* in the wild form to triploids (*D. intermedia* var. *fructuosa* (Gilb.) Wherry and *D.* × *boottii* (Tuckerm.) Und. respectively). *D. spinulosa* and *D. cristata* also hybridize together on the tetraploid level. Genuine *D. dilatata* (tetraploid) is not found in N. America unless represented by the species *D. campyloptera* (Kunze) Clarkson which is obviously closely allied to it and regarded by some authors as synonymous with it. *D. campyloptera* differs from European *D. dilatata* in that it is often eglandulate and has a prostrate rhizome as opposed to erect. The taxonomy of the entire complex is at present under consideration following cytogenetic investigation.

A number of other associated species occur in N. America and interspecific hybridization is rife which adds further complexity to the taxonomy of the genus. Three such species are diploid, *D. marginalis* (L.) Gray, *D. goldiana* (Hooker) Grey and *D. ludoviciana* (Kunze) Small. The former two are unrelated to and readily distinguished on gross morphology from species in the *D. spinulosa* complex, but *D. ludoviciana* is not unlike *D. cristata* except when fertile and then may be distinguished by its dimorphic fronds. *D. ludoviciana*, limited in distribution to S.E. coastal plain and Florida, may well prove to represent one of the other ancestral diploids in the *D. spinulosa* complex; experimental work is in progress to determine this.

D. marginalis links itself to the *D. spinulosa* complex via a diploid hybrid with *D. intermedia* and a triploid hybrid (*D.* × *slossonae* (Hahne) Wherry) with *D. cristata*. *D. goldiana* hybridizes with *D. cristata* also and with *D. marginalis* so that five species complete a ring of hybridization in the order *D. spinulosa—D. cristata—D. goldiana—D. marginalis—D. intermedia—D. spinulosa*.

From this ring arise further cases of speciation by allopolyploidy. *D. clintoniana* (D. C. Eaton) Dowell is one which, by various authors, has been regarded as a variety of *D. cristata*, as a hybrid between *D. cristata* and *D. goldiana* and as a distinct species. Cytologically it is a fertile hexaploid and morphologically is related to both *D. cristata* (a tetraploid) and *D. goldiana* (a diploid) from which it has arisen almost certainly by hybridization and chromosome doubling. *D. clintoniana* is reported to hybridize with every

species in the ring of five mentioned above but so far only two. *D. clintoniana* × *D. cristata* and *D. clintoniana* × *D. marginalis* have been cytologically examined

D. leedsii Wherry is considered as the hybrid between *D. goldiana* and *D. marginalis*. Plants of this taxon which have been investigated are, however, a mixture of sterile diploid hybrids (both putative parents are diploid) and fertile tetraploids. The similarity in their morphology suggests that the tetraploids have arisen by chromosome doubling from the diploid hybrids.

The name *D. celsa* (Palmer) Knowlton, Palmer & Pollard is generally applied to plants considered as hybrids between *D. goldiana* and *D. clintoniana*. Investigation shows, however, that *D. celsa* is a fully fertile species and tetraploid ; it is undoubtedly related to *D. goldiana* but not directly to *D. clintoniana*.

Based on cytological and morphological evidence, *D. clintoniana*, *D. leedsii* and *D. celsa* represent three allopolyploids each of which have *D. goldiana* as one of the original parent species. Further interspecific hybridization with other species and back-crossing to parent species has created a reticulate pattern of evolution in which intermediate individuals have arisen and provided difficulties in identification. A number of these intermediate forms are sterile hybrids which show complete lack of chromosome homology during meiosis. These provide a source for possible future development of new allopolyploid species which can only add to the present taxonomic complexity.

A more detailed report of the above investigations is being prepared for publication elsewhere.

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GENERAL DISCUSSION

The discussion began by Dr V. H. Heywood asking a number of questions. First, are taxonomists and experimental taxonomists pursuing the same aims ? Are they mainly interested in observing facts, or in predicting the future course of evolution ? Secondly, can one legitimately apply results obtained from experiments to what is observed in wild populations ? For example, can experiments on hybribization in the greenhouse have any real bearing on natural hybridization in wild populations ? The third question is whether the units of taxonomy are adequate and whether it is necessary to have more than one series of categories for the different kinds of information which are obtained. Dr Heywood seemed to think that many of the activities of the herbarium taxonomist and the experimental taxonomist were so different that it was difficult to translate experimental work into standard taxonomic terms. He emphasized the importance of retaining a morphological species definition and thought that the so-called biological definition, generally expressed in terms of populations and gene exchange, was best kept out of orthodox taxonomy.

Mr J. S. L. Gilmour agreed that there were considerable differences between taxonomy and what he would call the study of micro-evolution, but thought that in many ways they were complementary and could not be kept entirely separate.

Professor Valentine took up this point briefly ; he restated the definition of experimental taxonomy which he had proposed at the beginning of the

symposium, and insisted on the validity of experimental taxonomy as a scientific discipline, pointing out that this point was well exemplified by the papers which had just been given. Dr Heywood agreed that there should be no real difference between the so-called 'alpha' and 'omega' taxonomies and that all taxonomy is synthetic, but many leading experimental taxonomists kept them separate.

Dr Melville brought forward the question of nomenclature and suggested that in difficult cases stages were likely to arise within polyploid series where it might be convenient to have a special trinomial system in which a new category such as 'cyton' might be introduced to describe cytotypes. Dr Wilkins disagreed with Dr Melville's point. He thought that all the names which were used should be included in the taxonomic system, and that the fact that morphological and cytological groupings did not always coincide made the problem of classification in polyploid complexes such as *Festuca ovina* very difficult.

Dr Lovis then gave a summary of his views on the appropriate taxonomic treatment of *Asplenium trichomanes*, and suggested that at least three species corresponding to the diploid, tetraploid, and hexaploid levels could be made. Dr Walters asked him why he would give these taxa specific rather than subspecific status. Dr Lovis in reply thought that the fact that the taxa differed not only in morphology and cytology but also in ecology and geographical distribution justified specific status.

Dr R. Ross then spoke. He agreed that the taxonomist had to take into account all the available data in making his assessments. He also pointed out that it was important to make firm taxonomic decisions before dealing with questions of nomenclature.

Professor Holttum agreed with Dr Ross's point of view. He emphasized the extent of our ignorance in many important genera such as *Dryopteris* and thought that co-operation with workers in other fields was essential.

Dr Walters returned to the question of polyploid series in which there was a species complex with a number of cytodemes. Three situations could be envisaged. In the first, binomials were already in existence and there was no difficulty. In the second no morphological differences existed, and the question of taxonomic recognition did not arise. In the third, morphological differences, insufficiently large or clear to use for specific distinction, were present, and in this case he suggested that cytodemes should be given the status of sub-species. Professor Manton pointed out that much of the disagreement in applying a proposal of this kind arose from deciding what was a 'difficult' character, and what was an 'easy' character. Professor Valentine said that he preferred in some cases to give the cytodemes specific rank because they were often of considerable ecological or geographical importance. Raising their rank would emphasize their importance and make them more likely to be utilized by non-taxonomists.

A short discussion in which Professor Hewer and Dr Melville took part centered round the use of the term sub-species. Professor Hewer said that in zoological work, sub-species always had geographical significance. Dr Melville thought that in botanical work subspecies should be used as little as possible.

The question of the use of aggregates was finally discussed. Mr F. White emphasized the importance of retaining group names for critical species since ordinary users such as naturalists and teachers could not be expected to separate critical species, and needed an aggregate name. Dr Heywood, winding up the discussion, did not object to the use of the term aggregate, but thought that it use should be restricted and carefully defined. An aggregate should be a collection of recognized taxa of specific status and not a mere cover for a group of populations of various kinds which had not been taxonomically worked out.

D. H. V.

OBITUARIES

Mrs Elsie Wilkins Sexton, F.L.S., who died at Alfriston, Sussex, on 18 February 1959 in her ninety-first year, had been a Fellow of the Linnean Society for 43 years.

Born in Truro, Cornwall, on 27 April 1868, she studied at the Truro School of Art. On her marriage to Louis E. Sexton, a dental surgeon, she took up residence in Plymouth where she remained until 1957. An expert amateur photographer and an enthusiastic microscopist, her husband took up microphotography as a hobby with the late Dr E. J. Allen, Director of the Plymouth Marine Laboratory. Mrs Sexton's artistic talent was directed into scientific channels and her beautiful and accurate drawings of Polychaete worms illustrate some of Dr Allen's papers Although she had no formal scientific training, she became interested in Crustacea, chiefly the Amphipoda, and published over 30 scientific papers between 1908 and 1951. A great admirer of the late Rev T. R. R. Stebbing, a leading authority on Amphipoda, she modelled her systematic work on his monumental *Challenger* report. She did much to elucidate the complicated taxonomy of European species of Gammarids and made a detailed study of post-embryonic growth, moulting and intersexes in a number of species that occur in the Plymouth region. She became expert at rearing and breeding the animals under laboratory conditions. The discovery of a red-eyed mutant in *Gammarus chevreuxi* Sexton started a long series of experiments on the inheritance of eye-colour in that species. In this genetical work she collaborated with Dr Allen and with several younger scientists who helped with the exacting task of caring for numerous broods and examining thousands of specimens collected in the field for variations in eye-colour. The summary, which she published in 1936, of the work carried out on *Gammarus chevreuxi* at the Plymouth Laboratory since 1912 includes a fairly extensive bibliography.

From 1924 until 1947 she was on the staff of the Laboratory as Director's Research Assistant and as Zoologist. When war broke out she was given permission to do most of her work at home, with occasional visits to the Laboratory. Her correspondence with me began in December, 1939, when she was cut off from foreign Amphipod specialists. On 6 April 1942 she wrote (in her bold, firm handwriting) : ' I have finished the *Gammarus zaddachi* paper now and Dr Kemp wants me to finish *Jassa*. I did a lot of work some years ago [1928–1930] and collected 1,000 moults. Curiously enough, the blitz wiped out all the *Gammarus* I had, but spared most of the tubes containing *Jassa*.' She had always hoped to do more breeding experiments before writing up the *Jassa* work, but during the war that was impossible. With some assistance from D. M. Reid, a large manuscript was completed in six years. In the beginning of 1948 I met her for the first time, an octogenarian (almost) of charming and forceful personality, in her beautiful home surrounded by a botanic garden in miniature. For many years botanical correspondents in many lands, including Mexico, South Africa and Japan, had supplied her with rare plants which she delighted to cultivate. Although her eye-sight was failing, she had a remarkable memory and knew the extensive *Jassa* literature by heart. She hoped that the paper would appear in the *Transactions* of the Linnean Society, where the first description of *Jassa falcata* (Montagu) was published, and that her very detailed drawings would not be reduced too much. But publication of the *Transactions* was in abeyance and the text had to be drastically pruned to complete one number of the Journal (1951). I had a strong impression that her ' broad form ' and ' narrow form ' *Jassa falcata* belong to two distinct species, each of which undergoes striking morphological changes during growth. But that is for some future worker to prove or disprove.

Her daughter, who died in 1951, was also associated with the Marine Laboratory for many years as Assistant Librarian and as Librarian. She is survived by a son, Colonel F. B. W. Sexton, also a dentist, who resides at Alfriston.

ISABELLA GORDON.

By the death of **Professor Florence Annie Mockeridge** on 18 December 1958 at the age of 69, the Linnean Society loses a Fellow whose contributions to botanical knowledge will long be remembered and whose qualities as a teacher endeared her to generations of students at the University College of Swansea. Despite the fact that she struggled against indifferent health her contributions to the academic, administrative and social life of the College were outstanding.

Professor Mockeridge graduated from King's College, London, with First Class Honours in the Pass and Honours degrees of the University of London, in 1909 and 1910 respectively, and was awarded the Carter Gold Medal. From 1911 to 1917 she worked as a research student under the late Professor W. B. Bottomley in a pioneer field of nitrogen fixation by Azotobacter and on the 'auximones' of natural manures. Peat was used as a medium and trials were organized over a wide field. Her researches gained the D.Sc. of the University of London and she always spoke of these years with pleasure and enthusiasm. She continued the theme of her research while a member of the staff of Kings College (1917–1922) and added considerably to our knowledge of growth-promoting substances.

In 1922, in the newly-established University College of Swansea, Dr Mockeridge was appointed an Independent Lecturer in Biology. During the next 32 years she made contribution to the life of the College and its vigorous development. She was twice Dean of the Faculty of Science, she became Vice-Principal during 1949–1951 and she never spared herself in the service of the College. She knew her students intimately and took pleasure in their personal affairs as well as in their academic training. She became the first Professor of Botany in 1936 and she strove for many years for the establishment of separate Departments of Botany and Zoology with facilities for Honours Degrees in both subjects. This desire she saw fulfilled shortly before her retirement in 1954 when the new Natural Sciences Building which she had planned with meticulous care and foresight became a reality.

The gifts with which the whole student body, as well as her own students, marked her retirement, gave her very deep pleasure and one may indeed say of her 'she used gladly to do well'.

LILY NEWTON.

Sir Ralph Sneyd Pearson, Kt, C.I.G., LL.D., F.L.S., died at his home in Thame, Oxfordshire on 8 December 1958 at the age of 84. Thus passed yet another of the older members of the Indian Forest Service.

Ralph S. Pearson was one of the seven forestry men in the 1896–1898 batch at the Royal Indian Emergency College at Coopers Hill. The class might be called one of average quality and what it learnt was by the hard way, plodding work. But then the previous year was Troup's year and that set a standard difficult to compete with. Pearson was in Germany for the practical training in forestry in a small, mainly Scots pine *revier*, East of Berlin. However plodding the job it was done and no grumbling, and he was always a splendid companion and a great talker.

It was at the Forest Research Bureau, Dehra Dun, U.P., India that Pearson as Forest Economist did his best work and saw his research work grow from small beginnings, ill-housed, ill-equipped, under-staffed and with little money available to be the largest forestry research and educational centre in the Commonwealth. That and his books and many publications are monuments to his long years of solid work in the interests of Indian forestry.

It was most appropriate that having built up a successful organization at Dehra Dun, Sir Ralph should in 1925 be selected as first head of the new Forest Products Research Laboratory which was created under the Department of Scientific and Industrial Research in consequence of lessons learned in the First World War which emphasized the inadequacy of our equipment in that field. He remained in charge until 1933 when failing health caused him to retire but not before he had laid the foundations of another successful organization whose work was amply demonstrated in the Second World War.

Sir Ralph was made C.I.E. in 1920 and was Knighted in 1933 ; he received an honorary degree of LL.D. from the University of St Andrews. He was elected a Fellow of the Society in 1907.

He wrote several monographs on subjects connected with forest products but his chief work, in conjunction with the late H. R. Brown of New York State College of Forestry was ' The Commercial Timbers of India '. He was very popular with all who served with and under him.

Predeceased by his wife in 1938 he is survived by a daughter and two sons, one of whom, F. G. O. Pearson, is head of the Section of External Relations at Princes Risborough.

His funeral took place at Thame Parish Church on 12 December 1958.

W. McF. Robertson.

Captain Bertram Hanmer Bunbury Symons-Jeune, F.L.S., died in Jamaica in January 1959, aged 73 years.

After World War I he took up gardening as his health, undermined by wartime service, required him to work out of doors. He specialized in rock gardening, and in particular, he studied the natural strata of the stone with which he worked. For many years, he exhibited successfully at the Chelsea Flow Show, and his gardens there were enriched by many plants which he had personally collected, or raised, as exemplified by saxifrage ' Tumbling Waters ', one of his hybrids between *S. lingulata* and *S. longifolia*.

In later years, he turned his fertile mind to the garden phlox. raising them from a new strain of hybrids, and writing a book on the subject. However, as an author, he is best known for his book *Natural Rockgardening* which although written 25 years ago, is still widely read. For the last few years of his life he lived in Jamaica for health reasons, and whilst there devoted himself to bougainvillea, and was writing a treatise on them at the time of his death.

He was a Fellow from 1921–1929 and 1950–1959.

Giles Loder.

John William Saunt, A.L.S. (*honoris causa*), an entomologist well known in the Midlands and in the Isle of Wight, died on 11 July 1958 at the age of 77 years.

His interest in Natural History began when he was living near Nottingham in his early teens (there are a large number of his county records in Prof. Carr's *Natural History of Notts*). His interests were wide, covering entomology, ornithology, botany and gardening. As with many of us his entomological collecting commenced with the Lepidoptera but he soon began to concentrate on Hymenoptera in which he made extensive collections of bees, wasps, ichneumons and sawflies. During the later years of his life he worked almost entirely on the sawflies of which he had one of the best collections in the country. He was an exceptionally good field naturalist, being remarkably observant, with a wonderful eye for anything unusual ; on entering any room his first glance was always at the windows and often he would hurry to one with his tube and capture some unusual dipteron.

His love of natural history was entirely self-developed for no one in his family had any leaning towards the subject nor any knowledge of it, neither did he receive any help from his school, the ordinary primary one, for such subjects as biology and botany were not taught in his schooldays. Neither did he receive any teaching in the classic languages ; nevertheless he realized from the first the importance of scientific names, so forced himself to learn them and always used them. He used to say that for many years he ploughed a lonely furrow, but later on, as his work became known, he was in touch with experts, such as J. L. Perkins and R. B. Benson, in his particular groups.

In 1925 he was elected an Associate *honoris causa* of the Linnean Society, an honour which pleased him greatly.

Earning his livelihood as a wood-working machinist he was naturally clever with his hands ; he made his own cabinets and store-boxes and was a most skilful setter of insects. I well remember his giving a lecture to the Coventry Natural History Society at which he displayed a thousand micros all beautifully set. He would have made an excellent museum curator but unfortunately his lack of a university education debarred him from this.

He did not write or speak much but when he did he expressed himself very lucidly. His last note was on the sawfly *Athalia cornubiae* Bens. five records of which exist in Great Britain, three of them recorded by him. At my last meeting with him, in May 1958, he told me he had since taken a fourth.

He was also keenly interested in Cacti, of which he possessed a large collection.

Our sympathy goes to his wife and their three children.

A. H. Newton.

Richard Charles L'Estrange Burges, elected F.L.S. in 1939, died suddenly at his home in Birmingham in July, 1959, in his 59th year.

Whilst still a pupil at King Edward's High School, Birmingham, he developed an interest in field botany that was to last all his life. Although he was by profession a doctor of medicine, his hobby and passion was the study of the British flora, and especially the flora of the West Midlands.

Burgess joined the Birmingham Natural History and Philosophical Society in 1934, becoming a member of its Council in 1946 and President of the newly formed Botanical Section from 1948–1950. He was President of the Society in 1955/6 and had been Vice-President since that date.

Having joined the Botanical Society of the British Isles in 1931 he contributed to its reports on many occasions, served on its Council and Committees, and was this year elected a Vice-President.

His knowledge of the British Flora was very wide, and he gave great help and encouragement to the younger botanists in Birmingham, especially to the enthusiastic young naturalists at his old school, where he was Medical Officer. Burges also was keenly interested in the plants of the Alps and Pyrenees, and made many collecting trips to Europe in company with other botanists. His enthusiasm for native British species was matched by his interest in aliens, and in 1943 he contributed a paper to the Botanical Exchange Club Report entitled ' The Adventive Flora of Burton-on-Trent '. He also stimulated and played an important part in the Birmingham Natural History Society's survey of the post-war colonization of bombed sites in Birmingham which was published in the *Proceedings* of 1947.

It was no doubt his interest in the finer differences between critical groups of various genera—*Euphrasia*, *Hieracium*, *Potamogeton*, to mention but a few—which enabled him to recognize *Alisma gramineum* at Westwood Park, near Droitwich, as a distinct species new to Britain.

Burges took a great interest in the work in progress on the revision of the Flora of Warwickshire, even though, due to his large medical practice and his recent Chairmanship of the Birmingham division of the British Medical Association, he was not able to play an active part in this work.

His extensive and valuable library and herbarium, which have both been bequeathed to the Birmingham Natural History and Philosophical Society, demonstrate the great range of his interests. Burges was an amateur botanist in the best sense of the word, and his death will be felt keenly by all who knew him.

J. G. Hawkes.

The Linnean Society of London, Burlington House, Piccadilly, London, W.1.

NOTES FOR AUTHORS

Careful attention to these notes can accelerate consideration, acceptance and publication of papers.

1. Study the arrangement and conventions of the journal in which your paper is to appear.

2. *Papers* must be concise. Adventitious material, relevant in doctorial theses, is seldom acceptable for publication.

3. In addition to MS. of text, attach an *abstract* or *summary* of contents in triplicate of about 200/100 words, without any illustrations or references, on separate sheet of paper from main text.

4. Include a *Table of Contents*, whether publication is desired or not, on separate sheet of paper from main text. Table should show complete hierarchy of headings as discussed in note 6 below and have MS. folio numbers entered on it.

5. *Copy*, including legends for illustrations, graphs, etc., should be typewritten, double-spaced or, better still, treble-spaced, on one side of uniformly sized paper (Qto./Flscp.). Leave 1½ to 2 inch margin on left-hand side of each folio for printer's marks and editorial use generally.

Positions of all figures, graphs and tables must be indicated in left-hand margin; preferably they should all be referred to in the text.

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8. Underline *generic names* and *specific epithets* in text but leave unmarked in lists, tables, etc. Give author of name when it is first used or in most prominent place in text.

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J 1123 Standard Symbols

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In list of References the form should be:—Barlow, W. F. 1855. Observations on the respiratory movements of insects. *Phil. Trans.*, **145**: 139–148. (Underline vol. No. wavy to indicate bold face.)

Underline title of journal or book to indicate italic face. Wherever possible abbreviate titles of journals in accordance with *World List of Scientific Periodicals*. Do not abbreviate titles of books but add place of publication with indication of edition if other than first. In purely systematic papers subject-titles of papers in journals may be omitted at author's discretion or editorial decision.

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–	Pellage brown	4
2 (1)	Tail bushy; occurs only in *Auracaria* forest at altitudes above 5000 ft	**browni** Smith, p. 80
–	Tail naked; never in *Auracaria* forest	3
3 (2)	Nose pink	**robinsoni** Jones, p. 70
–	Nose black	5
4 (1)	Eyes blue	**jonesi** Robinson, p. 60
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